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ENGLAND.

THE PRE-NUPTIAL MIGRATION OF THE YELLOW WAGTAIL (*MOTACILLA FLAVA*) FROM LATITUDE 0·04′ N.

BY

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[Accepted 13th May 1958]

(With 1 figure in the text.)

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INTRODUCTION

It is generally believed that the pre-nuptial journey of migratory birds is under photoperiodic control. The possibility that this movement in trans-equatorial and equatorial migrants may be a function of a semi-autonomous internal rhythm of reproduction operating independently of photofluctuations has also been suggested (Baker, 1938; Marshall, 1951). Numerous migratory species avoid the northern winter by crossing the equator to southern continents and are reported to return with remarkable regularity. Although it is possible

Fig. 1.—Probable distribution and migratory routes of the Yellow Wagtails (*Motacilla*). These are *Budytes f. flavus* (left) and *B. t. thunbergi* (right) according to the nomenclature of Grant and Mackworth-Praed (1952). The spot on the equator indicates the Entebbe area where the present material was collected from October to April inclusive.

that they return in response to decreasing daylengths, the only experimental investigation yet carried out on transequatorial migrants has yielded no evidence of such an influence (Marshall & Serventy, 1959).

The individuals collected for use in the present study were " wintering " astride the equator (see map) where the total variation in daylength is of the order of about two minutes per annum. Thus, some individuals are subject to infinitesimal increases, and others to minute decreases, in photostimulation during their annual six months' stay on the equator.

MATERIALS AND METHODS

The present investigation is based on a mixed population of passerine Yellow Wagtails probably referable to *Budytes f. flavus* and *Budytes t. thunbergi* (Grant & Mackworth-Praed, 1952; Jackson, 1938). These birds, which are only dubiously distinguishable in the field (and often even in the laboratory), are sexually dimorphic. *B. f. flavus* (" Blue-headed " Yellow Wagtail) breeds in Scandinavia, France, middle Europe and the Caspian Sea. It " winters " over a wide area of Africa and Arabia. *B. t. thunbergi* (" Dark-headed " Yellow Wagtail) breeds in more northerly areas of Scandinavia than does the first-mentioned bird, as well as in Estonia and northern Russia (east to the Yenisei River). It migrates post-nuptially to Africa (as far south as Dumeraland and the Transvaal), Arabia, India, Burma and the Malay Peninsula.

The birds arrive on the northern shores of the Victoria Nyanza generally in the last days of September and return north in the second half of April. The material was taken (by M. C. W.) in the first place for the collection of serum between 25 October and 12 April during the years 1955–58 inclusive. All birds were taken within twelve miles in the Entebbe area where the total light increase between the December solstice and the departure date (approximately 18 April in 1957) is considerably less than half a minute.

The birds were collected by the use of a 0·410 shotgun and a ventral incision was made from sternum to vent. Each bird was now dropped whole into formal-calcium and labelled on return to the laboratory. Although inappropriate for detailed cytological study, this method of field preservation is quick and adequate for routine histological examination of spermatogenetic stages and lipid changes within the gonads. At the end of the collecting period the preserved material was air-mailed to London in polythene bags. Of the 113 birds collected, 92 were sufficiently undamaged by shot to be used as follows:

Plumage details, depot fat and stomach contents were recorded and the gonads were dissected out, measured and subjected to the following procedures: 1. One testis and half of each ovary were embedded in paraffin wax, sectioned at 6μ and stained with iron haemotoxylin for the demonstration of spermatogenetic stages. 2. The second testis and the other half of each ovary were embedded in gelatine, sectioned on the freezing microtome at 8μ and coloured with Sudan black for the investigation of lipid inclusions.

THE CONTRA-NUPTIAL ENVIRONMENT

Entebbe is situated on the northern shores of the Victoria Nyanza at an altitude of 3720 feet and possesses an unusually equable climate (Table 1).

TABLE 1

The Entebbe climate

*Mean rainfall in inches**

Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
2·57	3·57	6·27	10·08	9·60	4·77	3	2·95	2·95	3·74	5·17	4·57
*Average number of days of rain**											
9	11	16	22	23	14	10	12	11	13	17	12
Mean maximum temperatures in deg. F†											
80·1	79·7	79·2	78·0	77·0	76·7	76·0	76·9	78·3	79·3	79·0	78·7
Mean minimum temperatures in deg. F†											
63·7	64·3	64·5	64·9	64·6	63·3	61·8	61·8	62·3	63·3	63·6	63·2
Mean relative percentage humidity (at 08 hrs. 30 min)†											
85	85	86	86	87	86	86	87	85	82	84	85

* Calculated over a period of 50 years

† Calculated over a period of 15 years

Although people commonly speak of the " short " and " long " rains, the rainy seasons are too irregular in distribution and occurrence to constitute a regular " timing " factor in the lakeside environment. Further, there is no alteration of lush and parched conditions such as occurs in many parts of Africa. Temperature fluctuations are slight and, unless some specific special dietary component is significant, there is, as revealed by stomach contents, no considerable seasonal fluctuation in the insect food supply.

It would seem that no major external change occurs with sufficient regularity to enable a European landfall to be made at a specific time of the year. The Entebbe population was probably dispersing by 12th April and perhaps even before. Some birds were still present on 18th April, and none was seen at the end of the month. The days at about 18th April are only some twenty seconds longer than at the December solstice. It is inconceivable that the annual periodicity of any animal can be regulated by such a minute degree of photofluctuation.

CHANGES IN GONADS, FAT DEPOSITION, PLUMAGE AND BEHAVIOUR

During the early months of collection the birds congregated in large feeding flocks of sometimes fifty strong, although scattered groups of less than ten birds occurred.

25 *October*. Three males had testes about 1 mm. in diameter with tubules 60μ wide containing spermatogonia. Leydig cell nuclei were about 3μ in diameter. The ovarian mass of two females was about 3·5 × 2 mm. and the largest oocytes were 180μ in diameter. There was little depot fat. Both sexes had buffy lemon-yellow ventral plumage.

1 *November*. Two males and two females were equal in all respects to the October birds.

7–8 *January*. Testes of eight males measured between 0·8×0·5 and 1·5×1·0 mm. in diameter. Tubules measured from 40 to 60μ in diameter, those of some birds containing small remnants of post-nuptial lipids. No bird yet had even a fairly lipoidal interstitium. Three males already had the throat relatively bright yellow whereas the ventral surface of the remainder was generally buffy lemon-yellow. The nine females possessed follicles measuring up to 280μ in diameter, all being in some stage of atresia. The ovaries were therefore highly lipoidal. The ventral surface of one female was yellowish-buff, becoming brighter yellow on the abdomen and under tail coverts. The remaining females had buff under-parts becoming faintly yellow. The colour change in females appeared to be less advanced that that of the males.

No correlation could be observed between gonad condition and plumage change. The gonads were inactive, and plumage change was proceeding aphasically. Seasonal fat deposition had not begun. Only minor traces were evident, often around the omenta of the alimentary tract.

7–8 *March*. Four males possessed testes of the size and condition described above. Those of a fifth had enlarged very slightly although no mitoses were present. One bird still retained traces of post-nuptial tubule lipids. Five females were in much the same gonad condition as those of previous months but a sixth possessed oocytes that had slightly enlarged (about 220μ in diameter). Although only two of the eleven birds showed very minor gonad modification, the plumage in all had become appreciably brighter in colour and the sexes were now readily distinguishable. There was nevertheless great variation in the depth of colour in both sexes and the two birds that were very slightly advanced in sexual condition were no brighter than several others.

13 *March*. Of seven males only two showed distinct gonad enlargement (1·5×1·5 and 2·0×1·5 mm. respectively). Although no mitoses were seen, increased numbers of spermatogonia were present. There was in these individuals no increase in depot fat, and the bird with the biggest gonads was no more brightly yellow than the others. The five females had largest oocytes ranging from 180 to 230μ in diameter but in no case was any enlargement of overall ovarian mass detectable. A wide variation in plumage colour was still manifest in both sexes, some males still being equal to the January birds whilst others had become a brilliant canary yellow.

20–21 *March*. Of seven males, three showed gonad enlargement (1·25 to 2 mm. in diameter). Tubules ranged from 40–50 μ wide in the smaller testes (largest Leydig nuclei 4×3 μ) to 130 μ in the larger (with Leydig nuclei 4×3 μ). In one bird with inactive tubules 130 μ wide a Leydig cell mitosis was observed—a common phenomenon in reptiles (Volsoe, 1944 ; Marshall Woolf, 1957), but excessively rare in birds. Of five females, the largest oocytes of one were 300 μ in diameter but none showed overall enlargement in ovarian mass and all still possessed thread-like oviducts. For the first time depot fat was noted ; it occurred in two males only, of which one possessed enlarged testes. Both sexes still exhibited considerable plumage variation.

Some females, for example, showed only a minor deepening in ventral colour whilst others had become strikingly yellow.

Although odd birds had previously (13th March) shown very slight gonad modification it was in the present sample that the first unmistakable signs of sexual recrudescence in both sexes were clearly evident. During this period too, behavioural changes were noted : a greater social cohesion was manifest, and when a brightly plumaged bird was killed frequently another would fly up and inspect the cadaver.

27 *March*. Of seven males only three showed gonad enlargement (up to 2·5 mm. in diameter) with tubules 60 to 70 μ wide and Leydig cells with nuclei from 4×3 to 4×4 in diameter. (One bird contained spermatogonial mitoses). Six females still showed no macroscopic ovarian enlargement but the largest oocytes in one bird had reached a diameter of 400 μ. Oviducts were still thread-like and fat deposition remained slight. All birds now possessed richly yellow chests, but the females lacked the brilliance of the males. Nevertheless, both sexes showed variation in the depth of their nuptial colour.

5 *April*. Of five males, two possessed testes 2·5 mm. and the others about 1·5 mm. in diameter. Mitoses were plentiful and tubules measured up to 80–95 μ in diameter. Leydig nuclei were now sometimes 6 μ in diameter. The tubules of relatively unmodified males still however measured only 50–60 μ wide. Of seven females, two showed slight macroscopic ovarian enlargement yet possessed thread-like oviducts. The largest oocytes were now 380 μ in diameter. There was evident a great variation in fat deposition : most birds still showed only meagre amounts but five (of both sexes) had become heavily loaded with premigratory fat. In the females the fat deposition was as striking as oviducal enlargement was slight. Variation in plumage in both sexes was striking even at this late date although many individuals had reached what was probably very near the peak of brilliance.

12 *April*. Of four males, one possessed testes measuring $2{\cdot}5 \times 1{\cdot}5$ mm. and contained many mitotic spermatogonia (tubules 80–90 μ wide) whilst those of the remainder were still about 1·5 mm., or smaller, in diameter. In no male yet examined was there more than faint traces of lipids accumulated, or at any rate retained, in the Leydig cells. Two females still possessed small ovaries but oocytes were 300–400 μ in diameter. All birds now possessed depot fat, but in smaller quantities than some of those taken earlier in the month. Even at this late date appreciable plumage variation existed within each sex.

DISCUSSION

It would appear from the foregoing that, like the Red-billed Weaver-finch (*Quelea quelea*) (Witschi, 1935) the seasonal assumption of the nutpial plumage in Yellow Wagtails is independent of gonadal hormones. Males become bright yellow long before any sexual advancement (as indicated by spermatogenetic condition) occurs, and when the interstitial Leydig cells are still apparently inactive. Birds of both sexes are aphasic in the assumption of their bright nuptial plumage, the underlying factors of which are still uninvestigated in the present species. All that is known is that, by the time they

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become sexually active, both sexes are well on the way towards the complete assumption of their nuptial plumage.

After the seasonal sexual dimorphism was well-established, the equatorial population studied began to come slowly and asynchronously into an active sexual condition. There were indications of minor gonad modification in odd birds in the first week of March, but it was not until towards the middle of the month that the first spermatogonial mitoses, causing overall testis enlargement, were observed and then only in relatively few individuals. An increasing proportion of birds of both sexes showed minor sexual advancement throughout March and early April. Even on 12th April, when the last sample was taken, the gonads of the majority, though beginning to enlarge, were still very near the minimum size.

This wide temporal range in the seasonal initiation of reproductive processes seems to be an indication that, like the plumage change, the sexual recrudescence is under rhythmical control and uninfluenced by any specific, overall external stimulus. The wide disparity noted is probably due to variations in rhythm among individuals.

It seems very probable that the equatorial population is brought into a general reproductive and social synchronization by sexual behaviour engendered by the gonad development of individuals. It will be recalled that when Emlen & Lorenz (1942) implanted testosterone pellets into free-living Valley Quail (*Lophortyx californicus*) neighbouring *untreated* birds also came prematurely into sexual condition.

It was observed that the social behaviour of Yellow Wagtails did in fact change before the departure north. From 21st March (just after testicular enlargement was noted in several individuals) onwards, a greater social cohesion was discernible. Birds took flight more readily when disturbed. We found that pre-migratory changes in social organization were expressed quantitatively in our equatorial collecting results. Thus, when a brightly plumaged bird was killed, another now frequently flew up to inspect the cadaver with the result that an average of two birds, instead of the previous one, was obtained for the expenditure of every three cartridges.

In all months there falls at Entebbe more than 2·5 inches of rain. The environment therefore, is perennially lush and the wagtails leave for their European breeding grounds at a time when there is no shortage of food nor any other external change that appears to be disagreeable to them. They vacate an ecological niche that is not apparently filled by any incoming population.

We believe that the sexual cycle, and the time of migration, is governed by an endogenous rhythm of reproduction and this hypothesis receives added weight from a recent experiment by Marshall & Serventy (1959). Shearwaters (*Puffius tenuirostris*) that breed on Tasmanian islands and migrate to the Northern Hemisphere were caged and subjected to telescoped photofluctuations of the same order normally experienced by the birds *en route* between Tasmania, the equator, Japan, the Aleutians (where they pause) and later North America, and the equator on their return journey. Neither experimental nor control birds showed any sexual differences whatever. Yet individuals allowed to

survive the experiment later came into breeding condition at almost the same time as the free birds that had made the vast transequatorial journey.

An obvious modification of the above hypothesis is to believe that the equatorial population of wagtails, having come rhythmically into migratory condition, may be influenced to migrate by northbound passage migrants whose cycle had been more or less precisely " timed " far south of the equator by *decreasing* daylengths. Although we do not subscribe to this alternative, we cannot deny the possibility of its existence.

If the northern journey does, in fact occur as a phase of internal rhythm followed by a brief period of hormone-induced social and sexual synchronization, external stimuli must still operate at some point of the sexual cycle to keep it in phase with the northern spring. These may be the factors conducive to nest-building or some other sub-terminal phase of reproductive activity (Marshall, 1951, 1954). It is probably necessary for the cycle to be " anchored " at only one period of the year in order to keep it appropriately in step with the seasons so that the young will be hatched at the time most propitious for their survival. It is possible that a " late " European winter (compelling delayed reproduction) might result in a rhythmically late pre-nuptial migration from the equator. Jackson (1938) has evidence that variation in the northern departure date does in fact occur.

SUMMARY

1. Migratory European YellowWagtails (*Motacilla flava*) reach the equator in Africa late in September and great numbers " winter " there. These birds begin to come aphasically into bright sexual plumage before January. The gonads are then still inactive : the colour-change is apparently part of an endogenous rhythm.

2. There exists in the area of collection (Entebbe, Uganda) no obvious external stimulus that seems likely to initiate the pre-nuptial gonad advancement and migration to the European breeding grounds. In every month there falls more than 2·5 inches of rain : the environment is perennially lush. There is no seasonal shortage of insect food. Fluctuations in temperature and humidity are negligible. The first undeniable signs of gonad modification in both sexes occurred in the second week of March, when days are less than 15 seconds longer than at the December solstice. There was still wide variation in plumage colour. Some birds were already brilliant yellow, but no correlation between gonad and plumage condition was evident.

3. There is wide temporal variation in the seasonal initiation of gametogenesis and it is suggested that like plumage change, sexual recrudescence and fat deposition are under rhythmical control and uninfluenced by any particular overall, external stimulus. The marked variation between individuals is probably due to innate differences in rhythm.

4. It is believed that migration begins after a brief hormone-induced period of sexual and social synchronization. At the date of departure, days are still only about twenty seconds longer than at the December solstice : it is inconceivable that the migration is governed by photoperiodicity.

5. Nevertheless, external stimuli must still operate at some point of the sexual cycle to keep it in phase with the northern spring. These may be factors conducive to building or some other sub-terminal phase of reproductive activity.

ACKNOWLEDGMENTS

It is a pleasure to give thanks to Dr David Bargman, who criticised our remarks on climate ; to Mr C. W. Mackworth-Praed, who gave an opinion on the identity of imperfectly prepared specimens ; and to Dr G. W. Dolphin who made certain calculations relating to daylength. One of us (A. J. M.) is especially indebted to the Director (Mr R. S. A. Beauchamp) and staff of the East African Fisheries Research Organization Laboratory, Jinja, for many kindnesses while working there as a Visiting Scientist.

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ADDENDUM

Curry-Lindahl (1958) was able to separate various races and writes of three "physiological categories" wintering in the Belgian Congo. He concludes that an internal cycle seems to be genetically stabilized and "functions in a rhythm that is synchronized to conditions in the breeding areas....the timing of this internal cycle with all its physiological and biological implications seems to be, so to speak, determined by the latitude (climate) of the breeding area".

Curry-Lindahl, K. (1958). Internal timer and spring migration in an equatorial migrant, the Yellow Wagtail (*Motacilla flava*). *Ark. Zool.* (Ser. 2) **11**, 541.

ON THE ANATOMY OF A NEW DICYNODONT GENUS WITH EVIDENCE OF THE POSITION OF THE TYMPANUM

BY

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[Communicated by Dr F. R. Parrington.—Accepted 10th June, 1958]

(With 17 figures in the text)

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INTRODUCTION

The dicynodonts were the main terrestrial herbivores of the Permian, when they were extremely numerous and widespread, and a few genera are found in the Triassic. Their remains are most common in South Africa, where they are found throughout the Beaufort Series of the Karroo System. Rocks belonging to this System are also present in Tanganyika where, in the Ruhuhu Valley, they contain two fossiliferous strata (Stockley, 1932). In these strata, which Nowack (1937) calls the Upper and the Lower Bone-Bearing Series, occur vertebrates of Middle Triassic and Upper Permian age respectively (Haughton, 1932). The present paper deals with a dicynodont collected from the Lower Bone-Bearing Series by Dr F. R. Parrington of Cambridge. Other representatives of the fauna of this Series have been described by Parrington (1936, 1946 a, 1946 b, 1955), Broili & Schröder (1936 b), von Huene (1942, 1944, 1950), Boonstra (1953), Crompton (1955 a) and Panchen (1959).

The material consists of several skulls, with one of which is associated much of the post-cranial skeleton. The use of the acetic acid technique has made possible a thorough investigation of the morphology of the material, which has proved to be a new genus. Most of the material was collected near

the village of Kingori, and the new genus has accordingly been named *Kingoria*. Comparison with the other dicynodonts described from the Lower Bone-Bearing Series showed that von Huene had already (1942) described, under the name *Dicynodon nowacki*, some specimens which belong to the new genus *Kingoria*, and his specimens were found to be conspecific with the specimens collected by Parrington. The type species of the new genus is therefore *Kingoria nowacki* (von Huene).

Two factors have combined to render the classification of the Dicynodontia extremely complex. Firstly, dicynodont skulls are extremely common in the Karroo rocks, but very few post-cranial remains have been described; secondly, until the development of the acetic acid technique, detailed investigation of the structure of the skull was very difficult. The classification of the Dicynodontia has therefore been based largely on the size, shape and structure of the skull in dorsal view and on the dentition, together with occasional features such as the presence of bosses on the pineal or nasal regions. More extensive information is available in a few cases, notably in the large Triassic genera, but no attempt has in the past been made to summarise either the apparent uniformities or the apparent variations in the post-cranial structure of the group. The unusually extensive information which is available on the morphology of *Kingoria* has made it possible to compare this genus with all the earlier genera. Accordingly it has been possible to compose a generic diagnosis which embraces all the characters which have been used as diagnostic in earlier genera, or which appear, from a survey of the literature, to vary in the Dicynodontia as a whole.

DIAGNOSIS AND TAXONOMY OF **KINGORIA,** gen.n.

Registration number: Dr F. R. Parrington Collection. FRP/84.

Genotype: *Kingoria nowacki* (von Huene).

Generic Diagnosis: Small dicynodont, without precanine or post-canine teeth; canines present or absent. Skull oval in dorsal view, greatest width posterior to level of pineal foramen. Breadth of interorbital bar greater than breadth of intertemporal bar. Snout broad, without nasal ridges or bosses. No pineal boss. No postfrontal bone. Long narrow preparietal, surrounding anterior part of pineal foramen. Postorbitals cover lateral portions of intertemporal bar; parietals exposed between them, but this region is not concave from side to side, parietals instead forming median ridge, and there is sharp transition between this region and occiput. Parietals extend back postero-laterally from dorsal apex of occiput. Posterior end of zygomatic arch not expanded into lateral wing. Tabular present, extending almost to post-temporal fossa. Distinct tympanic process on distal end of posterior surface of paroccipital process. Stapes without stapedial foramen. Interpterygoid vacuity present, bordered by vomer and pterygoids. Pterygoid separated from maxilla by ectopterygoid. Palatine not forming part of secondary palate, just fails to meet premaxilla. Palatal surface of premaxilla does not bear pair of anterior ridges. Ascending portion of epipterygoid very slender, apparently not expanded dorsally to form part of lateral wall of braincase. Marked venous groove on anterior face of prootic. No unossified zone between

basioccipital and basisphenoid. Distinct sella turcica, entered by paired internal carotid canals. Dentaries anteriorly form upwardly-curving, blunt, tapering " beak ". Lateral surface of dentary bears strong prominent wing. Articular bears retro-articular process.

Six cervical vertebrae. Atlas neural arch paired, each with neural spine directed postero-dorsally and laterally. Dorsal vertebrae with well-developed metapophyses. Five sacral vertebrae. Cervical and anterior dorsal ribs double-headed, other ribs single-headed. No cleithrum. Lateral corners of sternum bear pair of dorsal bosses. Coracoid foramen between scapula and precoracoid. Well-developed scapular spine. No bony pelvic symphysis. Pubis and ischium posterior to ilium. Fourth sacral rib touches ischium.

Many of the above characters appear in other dicynodont genera, and only three of them are independently diagnostic of the genus *Kingoria*. These are the structure of the palate, of the lower jaw and of the sacrum.

In most dicynodont genera the anterior ramus of the pterygoid meets the palatine and ectopterygoid ; the palatine is the larger of these two, and in some genera aids in the formation of the secondary palate, bordering much of the inner side of the premaxilla, while the ectopterygoid is smaller and often displaced laterally. In *Kingoria*, however, the ectopterygoid forms nearly the whole of the anterior continuation of the anterior ramus of the pterygoid, and the palatine forms only the walls and roof of the internal nares. The palatine does not form any part of the secondary palate, and it just fails to meet the premaxilla.

The typical dicynodont lower jaw has a sharp cutting edge around its anterior end. This is quite unlike the lower jaw of *Kingoria*, which tapers anteriorly to a blunt point. A third type of lower jaw is known, that of the endothiodonts tapering anteriorly to a sharp point which fits into a median notch in the upper jaw, but this is equally distinct from that of *Kingoria*. The palate of *Kingoria* is unusual in that it does not possess the anterior stout rounded palatal ridges which are found in many dicynodont genera, and this may reasonably be correlated with the unusual nature of the lower jaw.

The other feature in which *Kingoria* is unlike any other known dicynodont is the character of the pelvis. In the Dicynodontia, and in primitive synapsids as a whole, the pelvis in side view is usually rather dumb-bell shaped. The acetabulum lies in a rather narrow " neck " between the dorsal expansion of the ilium and the ventral expansion of the ischium and pubis. In *Kingoria* there is no central constriction ; the ilium extends antero-dorsally from the acetabulum, and the pubis and ischium extend posteriorly from it ; and the antero-dorsal corner of the ischium touches the fourth sacral rib.

The generic diagnosis of *Kingoria* is sufficient to distinguish it from all dicynodont genera except *Dicynodon*. This latter genus has been generally treated as a repository for all " normal " postcanine-less dicynodonts. " Normal " in effect here merely means that the form under consideration has a skull whose intertemporal bar is neither very wide nor very narrow, which does not have a pineal boss, and which has a preparietal bone which borders only the anterior part of the pineal foramen ; the skull may be from 50 mm.

to 550 mm. in length and may be tusked or tuskless. The genus *Dicynodon* therefore contains within its large assemblage of species such a wide variety of skull sizes, shapes and patterns, that it is impossible to find any characters which will serve to distinguish all of them from *Kingoria*, since in many of these species neither the palate nor the lower jaw nor the sacrum are known. All that is known in these species is a short description of the skull and a figure of the dorsal aspect of the skull, and the distinction between *Kingoria* and these species therefore rests upon this information. Fortunately, *Kingoria* is unusual in that the breadth of the interorbital bar is much greater than the breadth of the intertemporal bar, and the great majority of the species of *Dicynodon* may on this basis be provisionally excluded from the genus *Kingoria*. Of the remaining few species, *D. whaitsi* (Broom, 1913) differs from *Kingoria* in that it is very much larger (skull length 530 mm.) and has postfrontal bones ; *D. ingens* (Broom, 1907) possesses the stout paired anterior palatal ridges which are absent in *Kingoria ; D. clarencei* (Broom, 1950) and *D. dutoiti* (Broom & Schepers, 1937) differ in possessing postfrontal bones ; and *D. howardi* (Broom, 1948) differs in its extremely long narrow skull and snout. It cannot be said that the reasons given for excluding these species from *Kingoria* are definitive ; all that can be said is that the small amount of available information does contain some points of difference from *Kingoria*.

The only species of *Dicynodon* in which the description (Broom & Robinson, 1948) suggested that it might belong to the genus *Kingoria* was *D. galecephalus* from the *Cistecephalus* Zone of South Africa. Through the kindness of Dr Brink of the Bernard Price Institute for Palaeontological Research, Johannesburg, it was possible to examine the type specimen, which proved to have the characteristic lower jaw of *Kingoria*. The skull is smaller than that of *K. nowacki*, its probable original length being about 115 mm. ; the width of the interorbital bar is closer to the width of the intertemporal bar than in *K. nowacki*, and the preparietal, unlike that of *K. nowacki*, is pointed anteriorly. It is therefore specifically different from *K. nowacki*, though its skull is too badly damaged and distorted for it to be possible to compare the two species in detail, and it may be referred to the genus *Kingoria* as *Kingoria galecephala* (Broom & Robinson).

GENERAL ANATOMY OF *KINGORIA*

A. *Skull and lower jaw*

Dorsal view (Fig. 1A)

The greatest length of the skull (taken in the midline from the snout to a line drawn between the posterior margins of the squamosals) was probably about 15 cms., and its greatest width about 10·5 cms. There is no sign of any nasal or prefrontal bosses, apart from a very low median swelling on the anterior part of the frontals. There is a slight circum-orbital ridge on the prefrontal and lacrimal bones. A median parietal ridge, though damaged in specimen no. FRP 84, is shown by other specimens ; it runs along the intertemporal bar and encloses the pineal foramen. This median ridge bears a median longitudinal groove, but below this there is no sign of a median

suture between the parietals. A pair of ridges extends antero-laterally from near the front of the pineal foramen, fading out towards the orbital margins.

No trace of a postfrontal is evident in the preserved parts of the skull, either superficially or in section.

A low ridge runs posteriorly from the upper end of the post-orbital bar ; this ridge rapidly becomes more pronounced so that, posteriorly from a level about 11·5 mm. in front of the pineal foramen, the postorbital and the

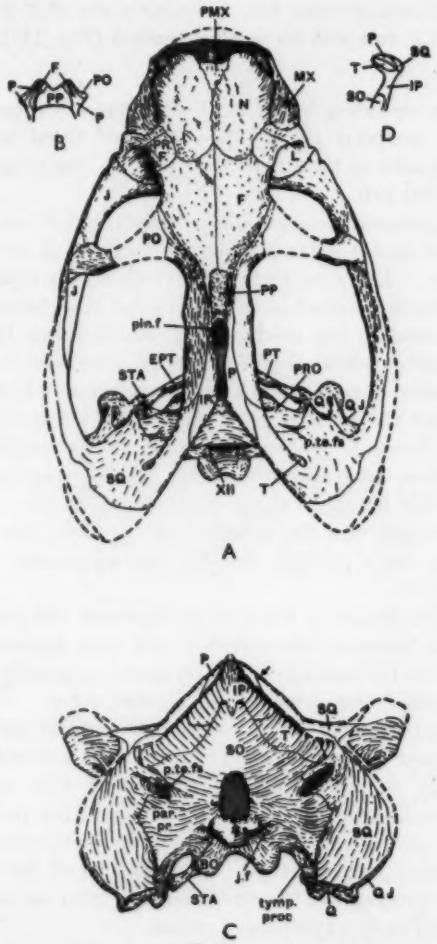

Fig. 1.—*Kingoria nowacki*, specimen no. 84. A, dorsal view of skull, $\times \frac{1}{2}$. B, section through intertemporal bar 1 cm. in front of pineal foramen, seen from behind, $\times \frac{1}{2}$. C, occipital view of skull, $\times \frac{1}{2}$. D, section through dorsal edge of occiput at point marked by arrow in C, $\times \frac{1}{2}$. j.f, jugular foramen; par.pr, paroccipital process; pin.f, pineal foramen; p.te.fs, post-temporal fossa; tymp.proc, tympanic process; XII, foramen for hypoglossal nerve. For abbreviations of names of bones, see p. 367.

parietal (upon which it is resting) together form a roof-like covering to the medial part of the temporal vacuity (Fig. 2B). More posteriorly, the squamosal replaces the postorbital as the superficial element in this structure, which finally merges into the dorsal border of the occiput. Even after this merging has taken place, the parietal continues to be present below the squamosal ; it thus extends a considerable distance postero-laterally beyond the dorsal apex of the occiput. This posterior extension of the parietal is almost completely hidden, being covered dorsally by the squamosal and posteriorly by the interparietal and tabular, but a slender strip of it is visible in anterior view (Fig. 2B), and it can also be seen in section (Fig. 1D).

Occipital view (Fig. 1C)

All the cartilage-replacing bones of the occiput are fused together to form a single unit, the occipital plate ; this is itself fused to the prootic and opisthotic, though traces of the suture between the basioccipital and opisthotic can be seen on the left side.

Dorsally the squamosal projects backwards about 8 mm. beyond the level of the occiput ; the under surface of this projection is covered by the interparietal and tabular. The structure of this region is complex (Fig. 1D). The meeting between the squamosal and the parietal (the former overlapping the latter) is wholly dorsal to the interparietal, which forms the whole thickness of the occipital plate below them. The situation is complicated by the intrusion of an antero-dorsal process of the tabular, which extends between the interparietal and the parietal to a point only a few millimetres from the dorsal apex of the occiput. In anterior view of the occipital plate (Fig. 2B) both the interparietal and, more ventrally, the supraoccipital, can be seen. In specimen no. FRP 84 there is an embayment in the medial wing of the squamosal, and through this the tabular can be seen ; this is not so in other specimens and may be a juvenile feature, the squamosal later consolidating the embayment.

Pairs of nutritive foramina are present between the interparietal and the supraoccipital and between the tabular and the squamosal. Each post-temporal fossa lies at the medial end of an antero-medially directed groove in the squamosal ; above this groove is a marked ridge.

The paroccipital process of the opisthotic is expanded distally, and buttresses against the squamosal and quadrate. Dorsally it is sutured to the squamosal, but more ventrally it merely lies against both the squamosal and the quadrate. The dorsal part of the occipital surface of the paroccipital process is hollowed, but the ventral part forms a tapering blunt rounded process, which projects about 7 mm. posterior to the general level of the surrounding bones. The nature of this process will be discussed in a later section ; for the present it will be referred to as the tympanic process.

Palatal view (Fig. 2A)

The most noticeable feature of the palate is the very long secondary palate, formed almost exclusively by the premaxilla. The pair of low blunt ridges found at the anterior end of the secondary palate in many dicynodonts is absent, but there is the normal posterior median ridge which leads to the

junction of the premaxilla and vomer. There is also a pair of sharp ridges, 1·5–2·0 mm. high, just medial to the premaxilla-maxilla suture ; these probably mark the internal limit of the original horny covering of the palate. There is a pair of low roughened areas on the postero-lateral corners of the palatal surface of the premaxilla. The internal surfaces of the maxilla, which form the sides of the buccal cavity, are rugose, there being a very large number of small and minute foramina. The edge of the maxilla in front of the canine is not a cutting edge, but is rounded.

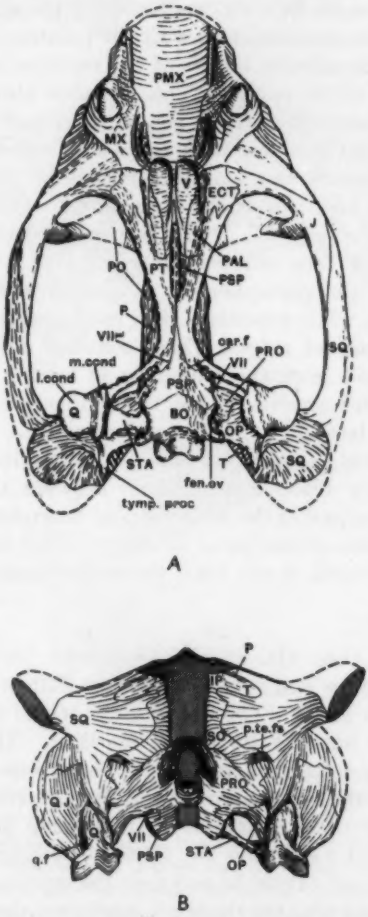

Fig. 2.—*Kingoria nowacki*, specimen no. 84. A, palatal view of skull, ×½. B, anterior view of hind part of skull, ×½. car.f, carotid foramen; fen.ov, fenestra ovalis; l.cond, lateral quadrate condyle; m.cond, medial quadrate condyle; p.te.fs, post-temporal fossa; q.f, quadrato-jugal foramen; tymp.proc, tympanic process; VII, foramen for facial nerve; VIIpal, foramen for palatine branch of facial nerve. For abreviations of names of bones, see p. 367.

The internal nares are sunk between high walls formed anteriorly by the palatines and posteriorly by the anterior rami of the pterygoids. The interpterygoid vacuity is long and narrow (20 mm. by 2·5 mm.); through it can be seen the ventral surface of the processus cultriformis of the parasphenoid. The anterior end of the pterygoid is firmly sutured to the large ectopterygoid. The ectopterygoid and the palatine are almost completely separated by a large foramen 5 mm. long; such a foramen is found also in *Cistecephalus* (Brink, 1950) and *Kannemeyeria* (Case, 1934). It is probably equivalent to the rather larger foramen, found in most reptiles, which Versluys (1936, p. 737) calls the lateral palatal fenestra, and which he considers probably transmits that ramus of the trigeminal nerve which communicates with the palatine nerve.

A deep notch in the anterior border of the palatine leads into the chamber surrounding the root of the canine. This chamber also opens into the nasal cavity through two foramina between the palatine and the maxilla (Fig. 4D). Posteriorly the nasal cavity is partially divided by a median septum formed by the vomer; more anteriorly this septum is formed by the premaxilla.

The parasphenoid and basisphenoid are fused together to form a " parasphenoid-basisphenoid complex "; it may be presumed that the usual Synapsid condition obtains here, the complex consisting of a basisphenoid portion covered ventrally by the parasphenoid. Posteriorly the parasphenoid overlaps the basioccipital, while anteriorly it is itself progressively overlapped by the pterygoids. A pair of ridges, which converge and join anteriorly, run along the parasphenoid from the basisphenoid tubera. The paired foramina for the internal carotid arteries pierce these ridges on their outer side, and thus open somewhat laterally. A pair of foramina lie in the pterygoids just anterior to the internal carotid foramina; a bristle inserted through one of these emerges dorsally through a foramen between the pterygoid and the lateral side of the dorsal part of the parasphenoid-basisphenoid complex (Fig. 3B, VII pal). The position of this canal is exactly what might be expected if it lodged the palatine branch of the facial nerve (Parrington & Westoll, 1940).

Side view (Fig. 3A, B)

The septomaxilla (Fig. 4D, E) is a small bone lying within the posterior part of the external naris and is very similar to that of *Dimetrodon* (Romer & Price, 1940, Plate 16 A–D). The dorsal edge of the bone is extended posteriorly to meet the anterior tip of the lacrimal. The body of the septomaxilla is pierced by a foramen and there are also two foramina, one above the other, between the septomaxilla and the maxilla. There are several possible explanations of the functions of these three foramina. A groove for the naso-lacrimal duct runs from the internal opening of the lacrimal canal forwards along the nasal cavity to end near the septomaxilla (Fig. 4D), but it is impossible to be sure whether the duct continued through the septomaxilla or through the upper foramen between the septomaxilla and the maxilla. Since the secondary palate of *Kingoria* has no foramen for a duct from the organ of Jacobsen, it seems unlikely that the organ could have had the function of sampling the contents of the buccal cavity, as it does in the modern Lepidosauria, and it is possible that one of the foramina in the region of the

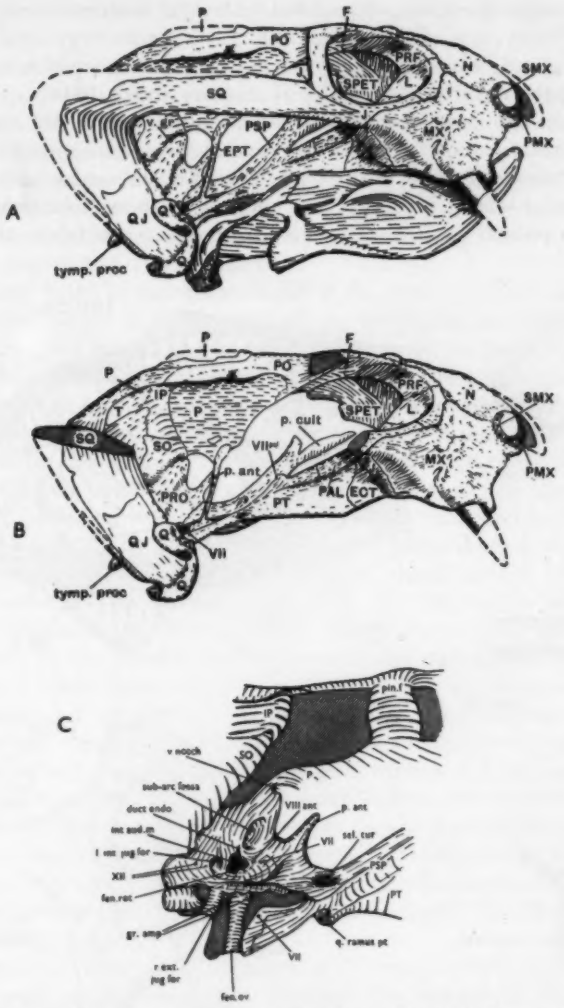

Fig. 3.—*Kingoria nowacki*, specimen no. 84. A, side view of skull and lower jaw, ×½. B, side view of skull after removal of zygomatic arch and post-orbital arch, ×½. C, internal view of braincase, viewed from right side, ×½. (Dorsally the section passes along the mid-line, ventrally it runs through the right jugular canal and the vestibule of the right inner ear.) duct.endo, ductus endolymphaticus; fen.ov, fenestra ovalis; fen.rot, fenestra rotunda; gr.amp, grooves leading to ampullar recesses; int.aud.m, internal auditory meatus; l.int. jug.for, internal opening of left jugular canal; p.ant, pila antotica; p.cult, processus cultriformis; pin.f, pineal foramen; q.ramus pt, quadrate ramus of pterygoid (cut); r.ext.jug.for, external opening of right jugular canal; sel.tur, sella turcica; sub-arc. fossa, sub-arcuate fossa; tymp.proc, tympanic process; v.gr, venous groove; v.notch, venous notch; VII, foramen for facial nerve; VIIpal, foramen for palatine branch of facial nerve; VIII ant, foramen for anterior branch of auditory nerve; XII, foramen for hypoglossal nerve. For abbreviations of names of bones, see p. 367.

septomaxilla might have been associated with some modification of the organ of Jacobsen. Finally, one of the foramina might have conveyed the duct of the lateral nasal gland, which in many lizards serves to keep the epithelium of the external naris covered with a film of mucous (Pratt, 1948).

As can been seen from the figures, the lateral surface of the maxilla shows various fine grooves and foramina, and several larger foramina lie in a deeper groove which runs antero-dorsally round the root of the canine tooth. Opening near the anterior end of the maxilla is another foramen, from which a groove runs onto the palatal surface of the maxilla, causing a notch in the margin of

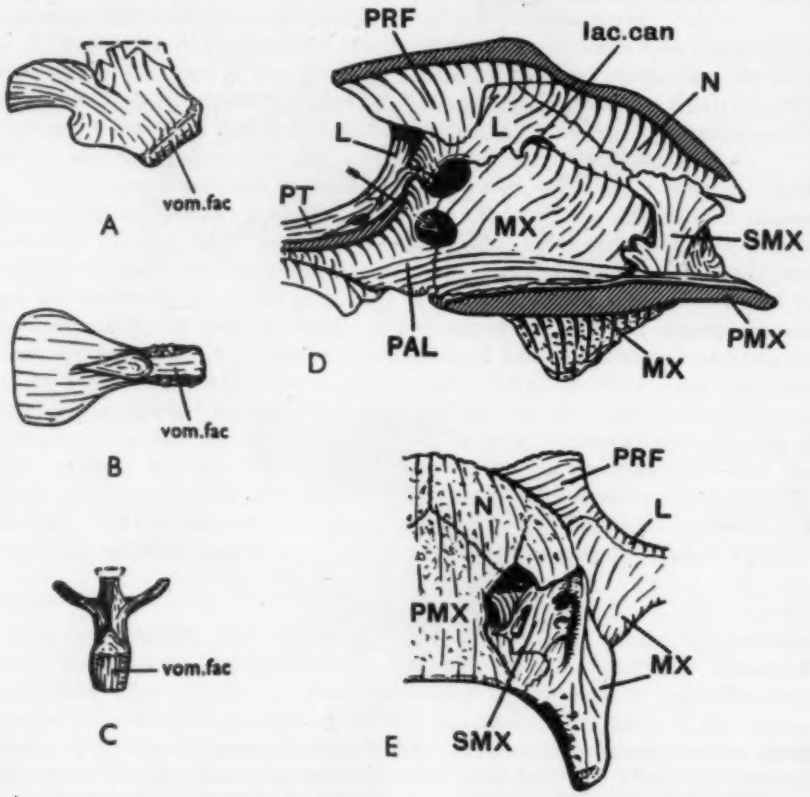

Fig. 4.—*Kingoria nowacki*. A–C, sphenethmoid of specimen no. 84, ×1. A, lateral view; B, ventral view; C, anterior view. D, medial view of left nasal cavity of specimen no. 76, ×1 (arrow runs through notch in palatine bone and into dental chamber). E, anterior view of region of left external naris of specimen no. 76, ×1. lac.can, internal opening of lacrimal canal; vom.fac, facet for vomer. For abbreviations of names of bones, see p. 367.

the bone; a bristle passed into this foramen emerges within the chamber surrounding the root of the canine tooth, just in front of the latter. It seems likely that all these foramina, and the porous nature of the palatal surface of

the maxilla, are concerned with the presence of a horny covering to this region during life.

Only two of the ten known East African specimens are tusked. One of the tuskless specimens shows no trace of a tusk even within the dental chamber. Since there do not appear to be any constant differences between the tusked and the tuskless specimens, they have provisionally been placed in the same species. If this is correct, tusks may have been borne only by the males.

There is a single lacrimal foramen 3·5 mm. high by 1·5 mm. wide. In the floor of the lacrimal canal is a foramen, from which a canal runs vertically through the roof of the dental chamber.

The median body of the sphenethmoid (Fig. 4, A–C) has a smooth antero-ventral surface, which is closely clasped by the dorsal surface of the vomer and is just touched by the antero-medial corners of the palatines. Both the postero-ventral surface of the sphenethmoid and the processus cultriformis, which meets it anteriorly, are grooved and they were probably joined in life by a cartilage which completed the inter-orbital septum. The body of the sphenethmoid meets the frontal dorsally and is expanded posteriorly to form a trough-like floor for the olfactory nerves. Contrary to the interpretation of Olson (1944), based on sectioned specimens, this expanded region shows no signs of being a separate ossification, and the sphenethmoid therefore is not divided into orbitosphenoid and mesethmoid. Olson further believed that a separate presphenoid ossification is present, but the region which he thus interprets in his specimens is in *Kingoria* merely the anterior part of the basi-sphenoid, lying in the processus cultriformis of the parasphenoid, and there is no sign of any other ossification equivalent to Olson's presphenoid.

The dorsal part of the suture between the parasphenoid–basisphenoid complex and the prootic is not very clear, but it appears to reach the edge of the cranial cavity just posterior to the sella turcica and just anterior to the base of the pila antotica, which is thus ossified from the prootic.

The anterior surface of the prootic bears a very marked groove (Fig. 3 A, v. gr.) about 4 mm. wide, which runs inwards, upwards and forwards from the anterior opening of the post-temporal fossa, to terminate anteriorly at a notch in the anterior edge of the wall of the braincase. The function of this groove is discussed later.

In side view the parietal continues vertically downwards to form the anterior part of the wall of the braincase. Though the sutures in this region are difficult to distinguish, the epipterygoid appears to take no part in the formation of this wall, its unexpanded upper end resting on the outer side of the parietal.

The upper portion of the laminar quadratojugal is immoveably slotted into the anterior face of the squamosal, and the lower portion is fused to the dorsal surface of the outer quadrate condyle ; there is thus no possibility of any kinetic movement of the quadrate. Above the point of fusion of the quadratojugal and quadrate the two bones are separated by the quadratojugal foramen, the posterior end of which is almost completely blocked by the squamosal. The quadrate consists of a large dorsal body and two ventral condyles. The rather bulbous body fits loosely into a pocket bordered

internally by the squamosal and paroccipital process and externally by the squamosal and quadratojugal. Its medial surface is rough and in life was probably joined to the squamosal by cartilage. The medial quadrate condyle projects posteriorly for about 3·5 mm. beyond the occipital surface of the squamosal and is visible through an embayment in the posterior edge of the squamosal and quadratojugal just above the outer condyle.

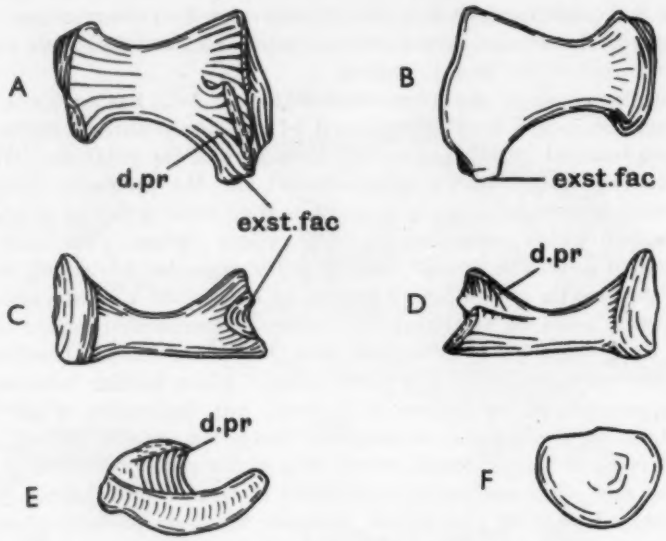

Fig. 5.—*Kingoria nowacki*, specimen no. 84. Right stapes, ×2½. A, dorsal view; B, ventral view; C, posterior view; D, anterior view; E, distal end; F, proximal end. Proximal end to left in A and C, to right in B and D. Anterior side uppermost in A and B, dorsal side uppermost in remainder. d.pr, dorsal process; exst.fac, extrastapedial facet.

The stapes (Fig. 5) lacks a stapedial foramen ; this may be usual in the Dicynodontia, as the only genera which have been reported to possess the foramen are *Cistecephalus* (Broili & Schröder, 1935 a) and *Eurychororhinus* (Broili & Schröder, 1935 b). The proximal end of the stapes is expanded into a footplate. The distal end is elongated and bears a groove which fits over a ridge on the inner surface of the medial quadrate condyle. On the right stapes this groove is continued onto a short posterior process, so that there is a postero-laterally directed facet, and it seems likely that this is for the base of an extrastapedial cartilage. This region is damaged in the left stapes. A dorsal process rises from the postero-lateral corner of the stapes and touches the ventral surface of the paroccipital process.

Braincase (Fig. 3C)

The prootic and opisthotic are almost completely fused together ; the only visible suture between them runs from the left fenestra ovalis dorso-laterally up the anterior face of the occipital plate (Fig. 2B).

The middle portion of the floor of the braincase bears a median ridge. At the level of the front edge of the internal auditory meatus this diverges into a pair of ridges which run antero-dorsally towards the pilae antoticae. Though they are rather far behind the sella turcica, it seems likely that these ridges represent the dorsum sellae medially and, more laterally, the alae basisphenoidales or clinoid processes, which normally run onto the bases of the pilae antoticae.

There is no sign of any unossified zone in the floor of the braincase, though such a zone was noted by Olson (1944) in some of his sectioned dicynodonts.

There are two notches in the ventral border of the internal auditory meatus. The more posterior of these is the fenestra rotunda ; the more anterior probably transmitted the posterior ramus of the auditory nerve. The anterior ramus of this nerve probably ran through a small foramen just anterior to the front end of the internal auditory meatus. A groove which runs up the wall of the braincase from the dorsal border of the internal auditory meatus probably lodged the ductus endolymphaticus.

There is no sign of any division of the vestibule of the inner ear into portions for the utriculus, sacculus and cochlea. The crus communis canalium runs into the vestibule just above the dorsal margin of the internal auditory meatus.

There is a very marked sub-arcuate fossa, which runs ventrally and postero-laterally into the wall of the braincase. It is about 5 mm. deep and its opening into the braincase is about 4 mm. in diameter.

Lower Jaw (Fig. 6)

As is usual in the Dicynodontia, there is no coronoid. No sutures are visible between the posterior ends of the articular, prearticular and surangular.

The two dentaries are fused anteriorly and together form the upturned beak, whose edges are rounded and lack a cutting edge. Posterior to this beak, the dorsal surface of the dentary forms a flattened area which, when the jaws are closed, touches the ectopterygoid and maxilla. Behind this, the dorsal surface divides into two ridges, the more lateral of which forms a strong ledge projecting from the side of the dentary. Between these two ridges is a marked concavity, and the form of this region suggests that it marks the point of insertion of a muscle.

The anterior portion of the angular bone is grooved ; the medial part of this groove receives the ventral edge of the splenial and prearticular, while the lateral part forms the floor of the meckelian fossa. This fossa extends anteriorly between the dentary and the prearticular. The splenial is applied to the medial side of the prearticular.

The reflected lamina of the angular extends ventro-medially around the lower margin of the jaw to form a well-developed horizontal component. The anterior end of the surangular is wedged into the inner surface of the dentary. The articular extends anteriorly as a thin lamina of bone between the surangular and the prearticular. The antero-ventral corner of this lamina bears a small facet for the reception of the posterior end of Meckel's cartilage

(Fig. 6F). The lateral articular condyle is produced ventrally to form a well-developed retro-articular process.

Part of the hyoid skeleton was preserved as a pair of slender rods, 2·4 cms. long, which lay between the rami of the lower jaw.

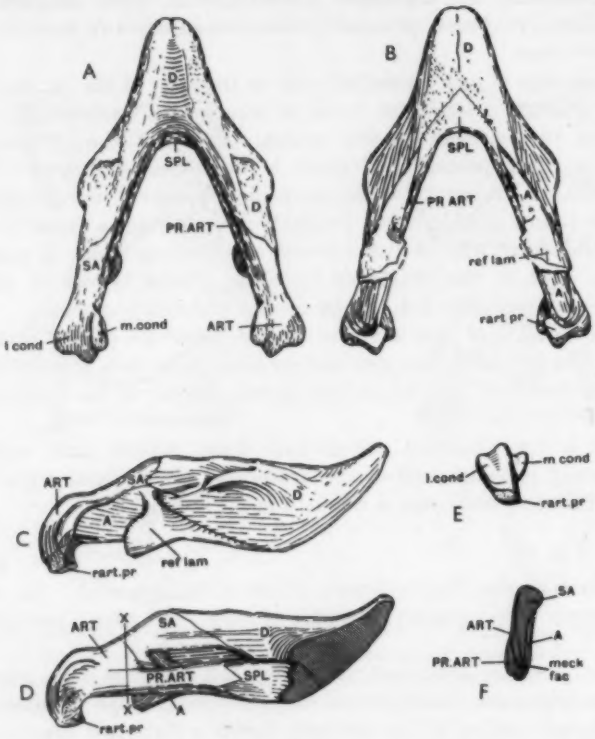

Fig. 6.—*Kingoria nowacki*, specimen no. 84. Lower jaw, ×½. A, dorsal view. B, ventral view. C, lateral view of right ramus. D, medial view of left ramus. E, posterior view of left articular region. F, anterior view of section taken at level X–X in figure D. l.cond, lateral articular condyle; m.cond, medial articular condyle; meck.fac, facet for posterior end of Meckel's cartilage; rart.pr, retro-articular process; ref.lam, reflected lamina of angular. For abbreviations of names of bones, see p. 367.

B. *Post-cranial skeleton*

The postcranial skeleton was preserved in three discontinuous blocks. The most anterior, block A, was attached to the back of the skull ; it contained the eleven most anterior vertebrae with their ribs, the pectoral girdle, complete except for the dorsal part of the right scapula, and the proximal parts of the humeri. The second block, B, contained fifteen dorsal vertebrae, with the dorsal parts of their ribs. The third block, C, contained the sacrum and the most anterior caudal vertebrae, and a portion of the head of the femur. The original relations of the bones were preserved almost unaltered.

Vertebral Column

The three blocks themselves contained the remains of thirty-four vertebrae, but other vertebrae may have been lost from between the blocks. Because the first vertebra of block B is very incomplete, the last vertebra of block A (itself damaged and distorted) can best be compared with the second vertebra of block B. The two appear to be very similar, so that there is no reason for assuming that any vertebrae have been lost from between these two blocks. The last vertebra of block A is dorsal vertebra 5, and the vertebrae of block B may therefore provisionally be regarded as dorsal vertebrae 6–21.

Only the posterior half of the first vertebra of block C is preserved and, because the posterior face of the centrum of this vertebra is enlarged to match the large anterior face of the first sacral vertebra, it is not readily comparable with the last vertebra of block B. However, it seems likely that few, if any, vertebrae are missing, since the number of presacral vertebrae actually present, twenty-seven, is already higher than that commonly reported in the Dicynodontia. Thus twenty-five presacral vertebrae have been reported in *Lystrosaurus* (Watson, 1912) and *Prolystrosaurus* (Haughton, 1917), twenty-six in *Dicynodon kolbei ?* (von Huene, 1931), *Aulacephalodon** (Olson & Byrne, 1938) and *Chelyposaurus* (Broom, 1905), twenty-eight in an unidentified species of *Dicynodon* (Broom, 1915) and thirty in *Dicynodon amalitzkii* (Sushkin, 1926).

Each centrum, throughout the column, has a small pit halfway along the floor of the neural canal ; in some cases this pit is paired. In the second sacral vertebra a pair of small canals connect the single pit to a pair of foramina on the sides of the centrum.

There are six cervical vertebrae, which can be distinguished from the dorsals by several features. The sizes of the parapophyses and diapophyses increase abruptly between vertebrae six and seven (Fig. 8A, B) and this is correlated with increases in the size of the rib-heads and in the thickness of the ribs. These increases may well indicate that the ribs of the seventh vertebra were the first to curve right round to meet the sternum, i.e. that it was the first dorsal vertebra, but unfortunately none of the ribs in this region is complete. Furthermore, as will be noted later, the intervertebral movements posterior to vertebra 6 are restricted and, finally, there is a noticeable difference between vertebrae 6 and 7 in the angle of the neural spines, that of 7 being more posteriorly directed.

Kingoria is the first dicynodont to provide clear evidence as to the number of cervical vertebrae.

The paired rod-like proatlas elements are 14 mm. long, each with a facet for articulation with the occiput but with no apparent facet for articulation with the atlas.

The atlas intercentrum was not preserved. The paired neural arch elements did not meet above the neural canal. There are clear facets for

* The correct spelling of this genus is as given above, Seeley (1898) having originated it as a sub-genus. Broom (1932) advanced it to the rank of a genus, but spelt it " *Aulacocephalodon* ", a spelling which has since been almost invariably used.

articulation with the occiput and axis, and there is a well-developed transverse process. In addition, there is a more dorsal process which is directed posterodorsally (Fig. 7) ; the identity of this will be discussed later. The atlas arches show no distinct facets for the proatlas or for the axis prezygapophyses.

The axis centrum shows a groove which marks the line of fusion of the axis proper and the atlas pleurocentrum. Anteriorly it bears facets for the three components of the atlas.

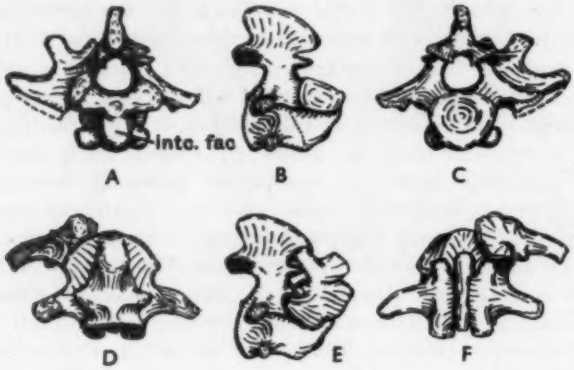

Fig. 7.—*Kingoria nowacki*, specimen no. 82. Axis, with right atlas neural arch added except in B, ×1. A, anterior view; B, E, lateral views; C, posterior view; D, ventral view; F, dorsal view. intc.fac, facet for atlas intercentrum.

Moving posteriorly, various progressive changes occur in the parapophyses and the transverse processes of the anterior vertebrae. The parapophyses become larger, and their position on the side of the centrum becomes more dorsal. The transverse process also becomes more dorsally directed. The facet for the tubercular rib-head is very large in the first three dorsal vertebrae, but in the fourth this facet is smaller, is further down the outer side of the now dorso-laterally directed transverse process, and is continuous with the parapophysis (Fig. 8B). This change in the position of the facet for the tuberculum is not accompanied by a similar change in the position of the transverse process as a whole. As a result, in the more posterior dorsal vertebrae this extends dorso-laterally as a rounded process which has no connection with the rib-head (Fig. 8C). It is thus no longer a transverse process in either orientation or function and, by comparison with Gadow's (1933) definitions of the various processes of vertebrae, it seems to be best described as a metapophysis.

The metapophyses appear to be normal characteristics of the Dicynodontia, though this fact has not hitherto been recognised. They can be seen in figures of the vertebrae of *Dicynodon tigriceps* (Owen, 1845), *D. pardiceps* (Owen, 1876, Plate 53), *Oudenodon gracilis* (Broom, 1901) and in the vertebrae of the specimen of *Dicynodon halli* described by Watson (1917). They were first described by Seeley (1900) in *Dicynodon leptoscelus*, are noted in *Kannemeyeria* by Pearson (1924 b), and appear to be present also in *Stahleckeria* (Camp &

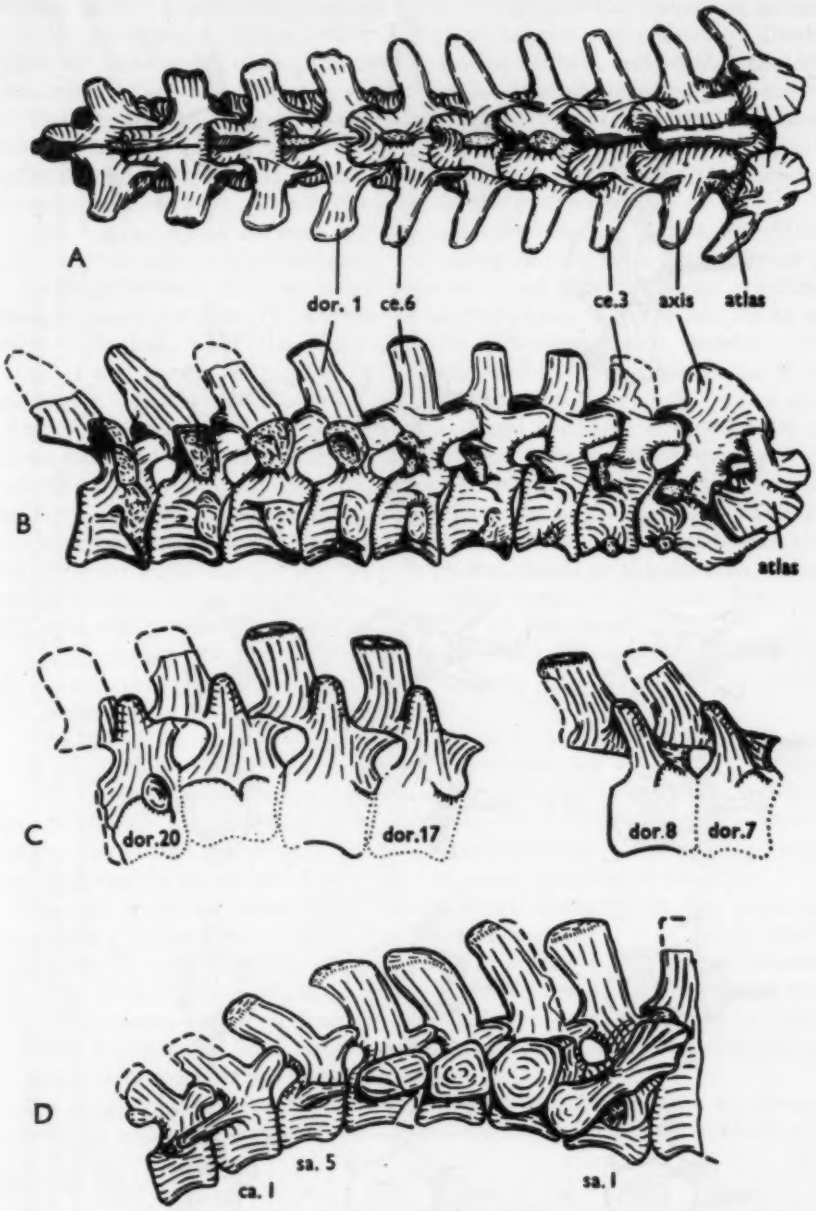

Fig. 8.—*Kingoria nowacki*, specimen no. 82. Vertebral column, ×1. A, dorsal and B, lateral, views of vertebrae from block A. C, lateral view of some vertebrae from block B. D, lateral view of vertebrae from block C. ca, caudal vertebra; ce, cervical vertebra; dor, dorsal vertebra; sa, sacral vertebra.

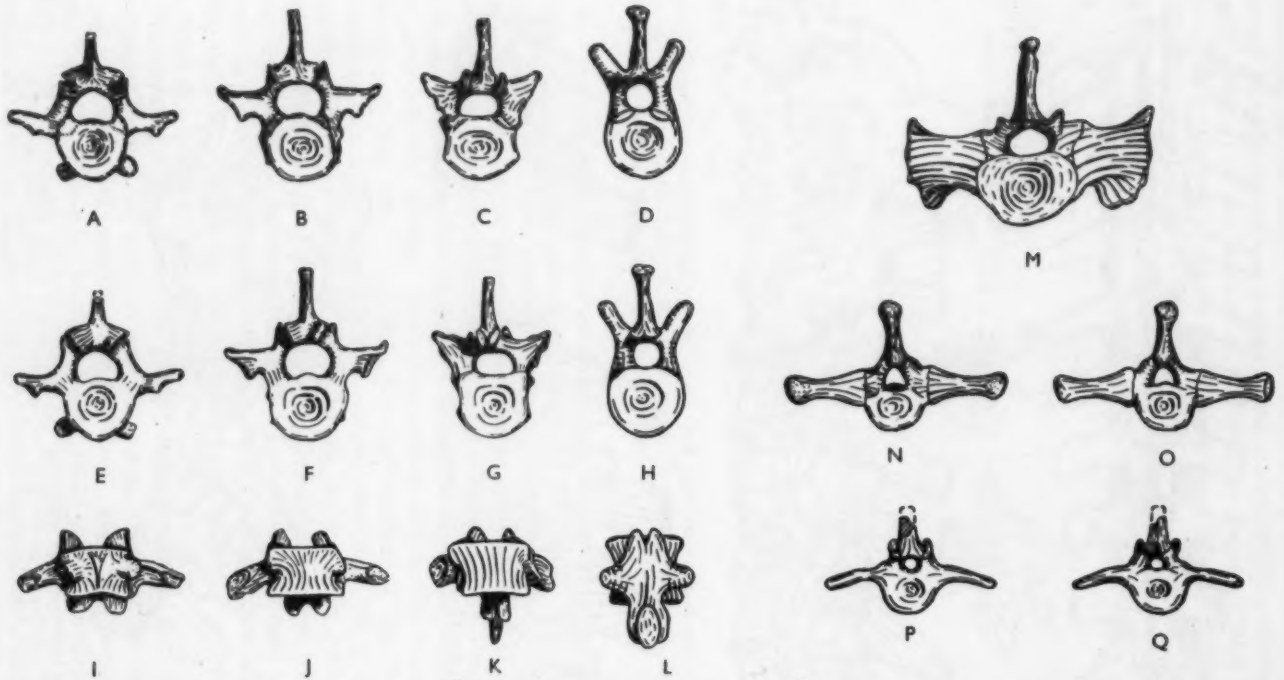

Fig. 9.—*Kingoria nowacki*, specimen no. 82. Vertebrae, ×1. A, E, I, third cervical vertebra; B, F, J, sixth cervical vertebra; C, G, K, second dorsal vertebra; D, H, L, eighteenth dorsal vertebra; M, first sacral vertebra and ribs; N, O, fourth sacral vertebra and ribs; P, Q, first caudal vertebra and ribs. A–D, M, N, P, anterior views. E–H, O, Q, posterior views. I–K, ventral views. L, dorsal view.

Welles, 1956). A progressive change in the direction of the transverse process is noted by Olson & Byrne (1938) in *Aulacephalodon* and figured by Broom (1905) in *Endothiodon*, though in both cases the authors believe that the ribs continued to be attached to the resulting dorso-laterally directed processes.

Though the Dicynodontia were bulky herbivorous animals, the bony sternum is very short, and this condition may have resulted in special modifications of the dorsal musculature to support the ribs and the enclosed viscera, and thus led to the development of the metapophyses.

The zygapophyses between the cervical vertebrae are set at an obtuse angle to each other and so permit both rotatory and dorso-ventral movement, as do those between the last cervical vertebra and the first dorsal vertebra. The zygapophyses of all the anterior dorsal vertebrae, however, are set at an acute angle but, while those between the first three dorsal vertebrae are flattened and permit only dorso-ventral movement, those between the third and fourth dorsal vertebrae are rounded and permit both dorso-ventral and rotatory movements. Thus the first three dorsal vertebrae cannot rotate on one another but there is free movement between them and both the cervicals and the more posterior dorsals. This may be related to the fact that, unlike the more posterior dorsal vertebrae, they have double-headed ribs. This in turn may be correlated with the very short sternum, and it is possible that the ribs of dorsal vertebrae 1–3 are the only ones attached to the sternum. This interpretation is supported by some dicynodont sterna in Professor Watson's collection which show three pairs of facets for rib attachment.

The centra of the dorsal vertebrae from block B are covered ventrally by a very thin layer of acid-resistant matrix, and they have therefore been indicated by dotted lines in Figure 8C.

Four sacral vertebrae have ribs with extensive bracing contacts with the pelvis (Fig. 8D). A fifth, more posterior, vertebra has ribs which, though slender, are directed antero-laterally, and the zygapophyses of this vertebra indicate that its movements were restricted to the vertical plane; it is therefore considered that this vertebra and its ribs are sufficiently modified for them to be regarded as sacral, and the number of sacral vertebrae is thus five.

The ribs of all the sacral vertebrae are fused to the centra, the point of fusion being marked by a slight dilation and rugosity. The first is much larger than the others, being elongated antero-dorsally; the postero-ventral end of its distal surface abuts against a projection on the inner side of the ilium. The distal end of the fourth rib is divided into two facets, the anterior of which touches the ilium while the posterior touches a marked facet on the antero-dorsal corner of the ischium.

The zygapophyses between caudal vertebra 1 and 2 are set at an obtuse angle to one another, permitting both dorso-ventral and rotatory movements.

Ribs (Fig. 10)

No trace was found of atlantal ribs, though both may have been lost with the atlas intercentrum. The preserved cervical ribs and the first three dorsal ribs are double-headed, while the remaining dorsal ribs are single-headed and appear to attach low down on the anterior part of the side of the centrum.

Such single-headed dorsal ribs appear to be normal in the Dicynodontia, and have been reported in various genera. However, double-headed dorsal ribs have been reported by Sushkin (1926) in *Dicynodon amalitzkii* and by Olson & Byrne (1938) in *Aulacephalodon*. In the latter case, the authors also state that the attachment to the centrum becomes intervertebral in the dorsal vertebrae, and this is also reported in *Endothiodon* by Broom (1905).

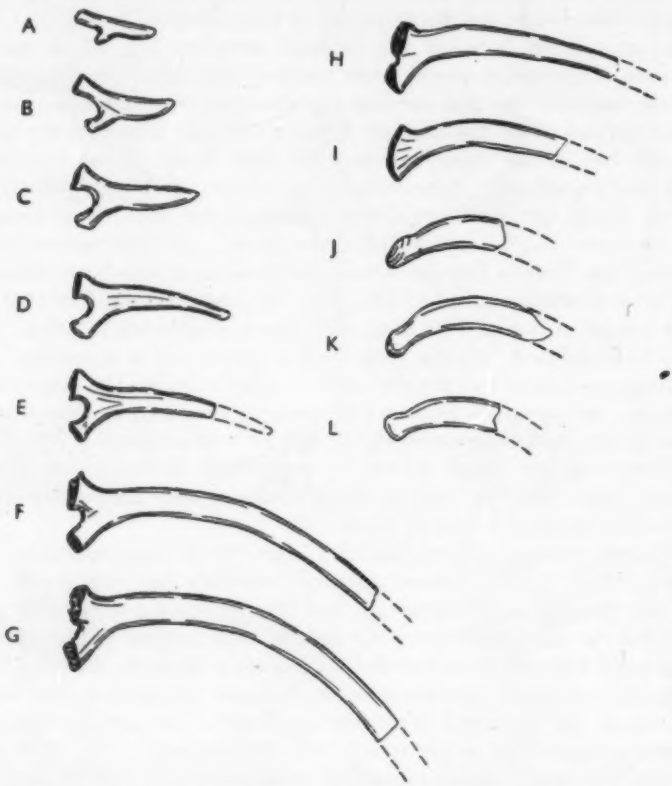

Fig. 10.—*Kingoria nowacki*, specimen no. 82. Posterior views of right ribs, ×1. A–E, cervical ribs; F–I, dorsal ribs 1–4; J, K, L, dorsal ribs 7, 11, 19.

Pectoral Girdle

There was no trace of a cleithrum, though the pectoral girdle was well preserved and undisturbed, neither does the scapula show any facet for such a bone. It therefore seems extremely likely that *Kingoria* did not possess a cleithrum, and that its absence is not merely a post-mortem condition. An examination of the literature shows that, though it is commonly stated that a cleithrum is present in the Dicynodontia, the evidence for this is extremely limited. The bone has been described in an unidentified dicynodont (Broom, 1915), in *Dicynodon amalitzkii* (Sushkin, 1926), in *Cistecephalus* (von Huene,

1942) and in *Kannemeyeria* (Watson, 1917; Pearson, 1924b). A groove, running down the anterior face of a scapula of *Stahleckeria*, was thought by von Huene (1935) to be for the cleithrum, but Romer & Price (1944) remark that it is absent in von Huene's two remaining specimens and also in their own additional specimen, and they consider that the groove was due to post-mortem crushing.

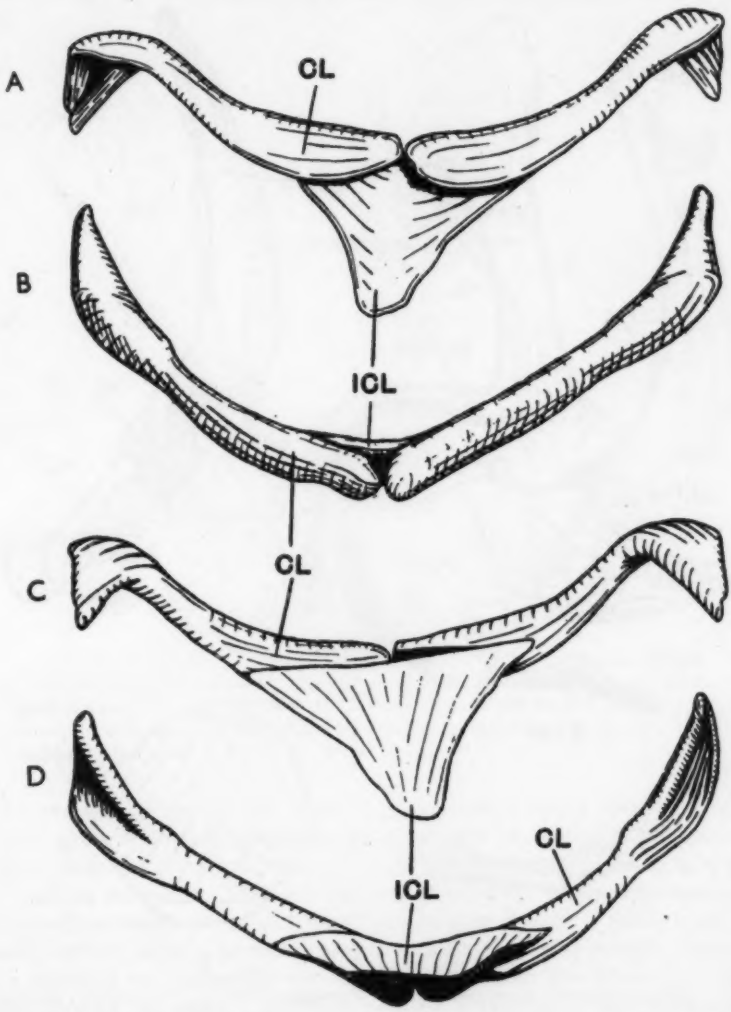

Fig. 11.—*Kingoria nowacki*, specimen no. 82. Clavicles and interclavicle, ×1. A, ventral view; B, anterior view; C, dorsal view; D, posterior view. For abbreviations of names of bones, see p. 367.

In other cases where pectoral girdles have been described, and no cleithrum has been found, it has generally been assumed that the bone has been lost during fossilisation. Though this small bone may well be less commonly collected than the other, larger, bones of the pectoral girdle, the above strong evidence that *Kingoria* did not possess a cleithrum suggests that its absence may be a more widespread phenomenon in the Dicynodontia than has hitherto been thought.

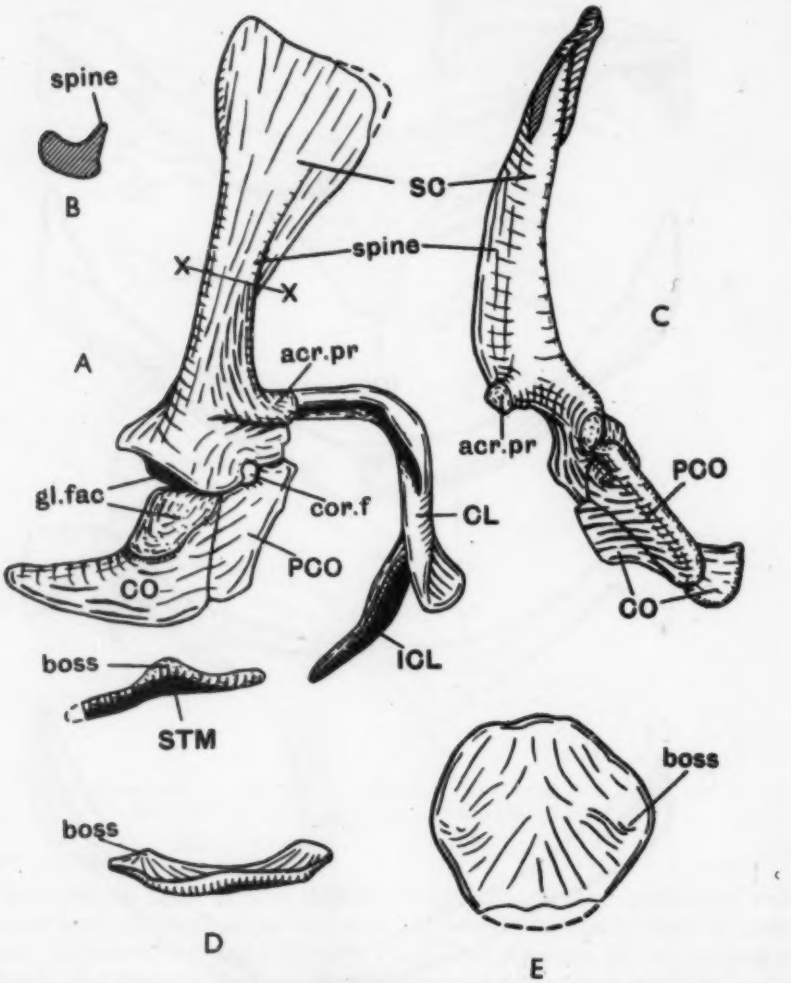

Fig. 12.—*Kingoria nowacki*, specimen no. 82. Pectoral girdle, ×1. A, whole pectoral girdle from right side; B, section through scapula taken at level X–X in figure A; C, anterior view of right scapula and coracoid plate; D, anterior and E, dorsal, views of sternum. acr.pr, acromion process; cor.f, coracoid foramen; gl.fac, glenoid facet. For abbreviations of names of bones, see p. 367.

The two clavicles could not be detached from the interclavicle and were slightly asymmetrical, so the three bones have been figured as preserved (Fig. 11). The interclavicle has no perichondral bone surface.

The posterior border of the hexagonal sternum (Fig. 12A, D, E) is damaged, and most of its ventral surface is eroded. On its dorsal surface, the lateral corners are raised into a pair of bosses, which may represent the anterior limit of the area of attachment of ribs to the bony sternum. Similar bosses have been described in *Platypodosaurus* (Owen, 1880) and *Placerias* (Camp & Welles, 1956).

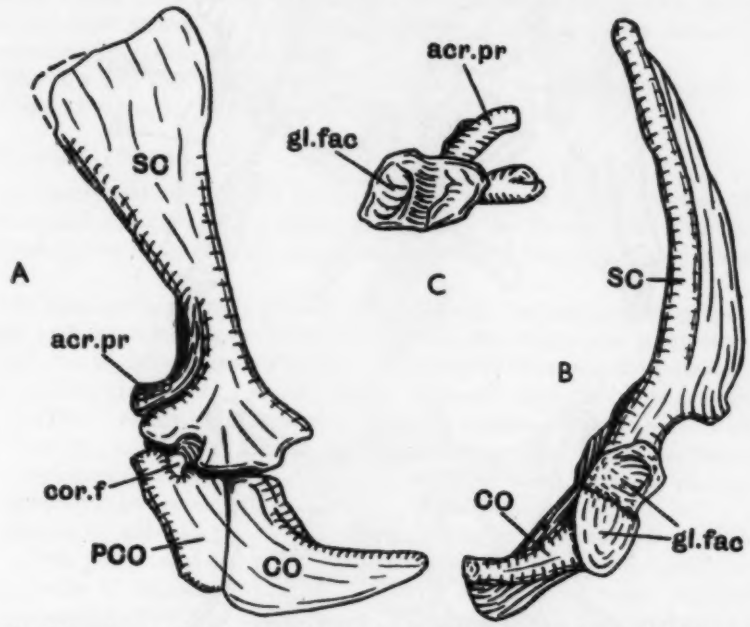

Fig. 13.—*Kingoria nowacki*, specimen no. 82. A, B, right scapula and coracoid plate, ×1; A, internal view; B, posterior view. C, ventral view of ventral end of right scapula, ×1. acr.pr, acromion process; cor.f, coracoid foramen; gl.fac, glenoid facet. For abbreviations of names of bones, see p. 367.

The scapula (Figs. 12, 13) bears a very marked spine running from the acromion process dorsally along the anterior part of the outer surface of the scapular blade. Though it thus possesses a scapular spine, which is today found only in mammals, *Kingoria* does not possess the prespinous area, which in mammals serves as the origin of a supraspinatus muscle. Though the spine probably served mainly as the insertion of the trapezius muscle, there is a groove running up under the acromion process onto the lower part of the anterior face of the spine. *Kingoria* may thus also have been mammal-like in possessing the beginnings of a supraspinatus muscle (which Watson (1917) stated was present in *Dicynodon halli*), resulting from a dorsal migration of the supracoracoideus muscle (see Romer, 1922). However, it does not seem

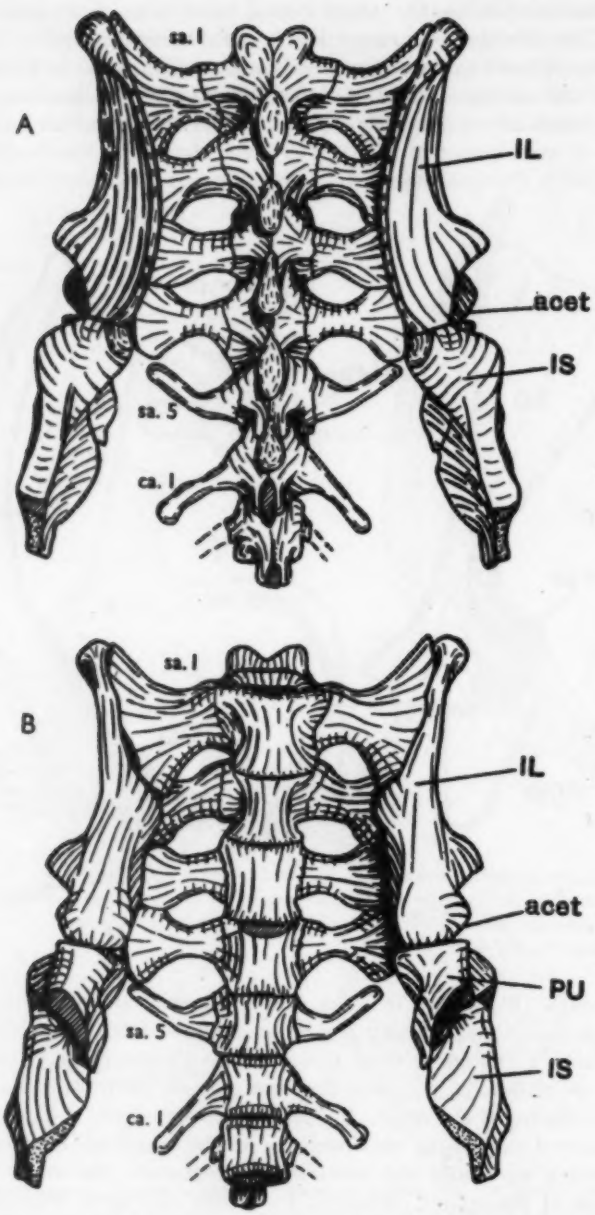

Fig. 14.—*Kingoria nowacki*, specimen no. 82. Sacrum, ×1. A, dorsal view; B, ventral view. acet, acetabulum; ca., caudal vertebra; sa., sacral vertebra. For abbreviations of names of bones, see p. 367.

to have possessed the similarly derived infraspinatus muscle, since ventral access to the scapular blade behind the spine is blocked by the base of the spine. This possibility that the anterior part of the supracoracoideus had gained an origin from the scapular blade before its posterior part had done so may be correlated with the unusual posture of the scapula. Watson (1917) first suggested that the dicynodont scapula had a marked anterior orientation, and this appears to have been the case in *Kingoria* (Fig. 12A).

The only other dicynodont in which a scapular spine has been described is the South American Middle Triassic genus *Stahleckeria* (Romer & Price, 1944), and the Upper Permian *Kingoria* is surprisingly advanced in this character. Two unrelated genera of dicynodonts have thus independently achieved the mammalian condition in this character.

The coracoid foramen lies between the scapula and the precoracoid. The precoracoid takes no part in the formation of the glenoid.

Pelvic Girdle (Figs 14, 15)

As mentioned earlier, the pelvic girdle is unusual in the position of the ischium and pubis, which are wholly posterior to the ilium. This situation has resulted in the antero-dorsal corner of the ischium meeting the fourth sacral rib.

The small pubis is firmly joined to the ischium; the large obturator foramen, 4 mm. high by 8 mm. wide, runs between the two bones and is directed posteriorly and slightly ventro-laterally. The junction between the puboischiadic plate and the ilium is not a sutural union; the surfaces of the bones are smooth, and the ilium readily separates from the other two bones. Combined with the fact that the junction is almost straight, this suggests that there may have been movement between the ilium and the pubo-ischiadic plate during life; alternatively, the specimen may not have been mature.

There is no sign of a pubic tubercle, but a scar on the outer side of the lower part of the pubis may mark its original position. The posterior and postero-ventral edge of the ischium is not covered by perichondral bone; this may be due to damage, or to tendons having been inserted on this edge, and the surface has been indicated by a dotted area in the figures.

The acetabulum is quite deep; its anterior border bears a particularly strong and rounded projection from which a ridge, apparently separating two areas of muscle attachment, runs anteriorly along the surface of the iliac blade. The region above this ridge was presumably for the ilio-femoralis muscle, which normally originates from this part of the ilium in amniotes. In living reptiles there is no muscle attached to the iliac blade ventral to this muscle, but in mammals this region has been invaded by part of the pubo-ischio-femoralis internus muscle. In reptiles this muscle runs from the anterior internal surface of the pubis to insert on the femur, but the changes in limb posture which took place during the evolution of mammals have led, as shown by Romer (1922), to a movement of this muscle to a more dorsal position in order to retain its original function of supporting the limb. In the course of this dorsal movement it has split into two components; the component attached to the lumbar vertebrae is known in mammals as the psoas major,

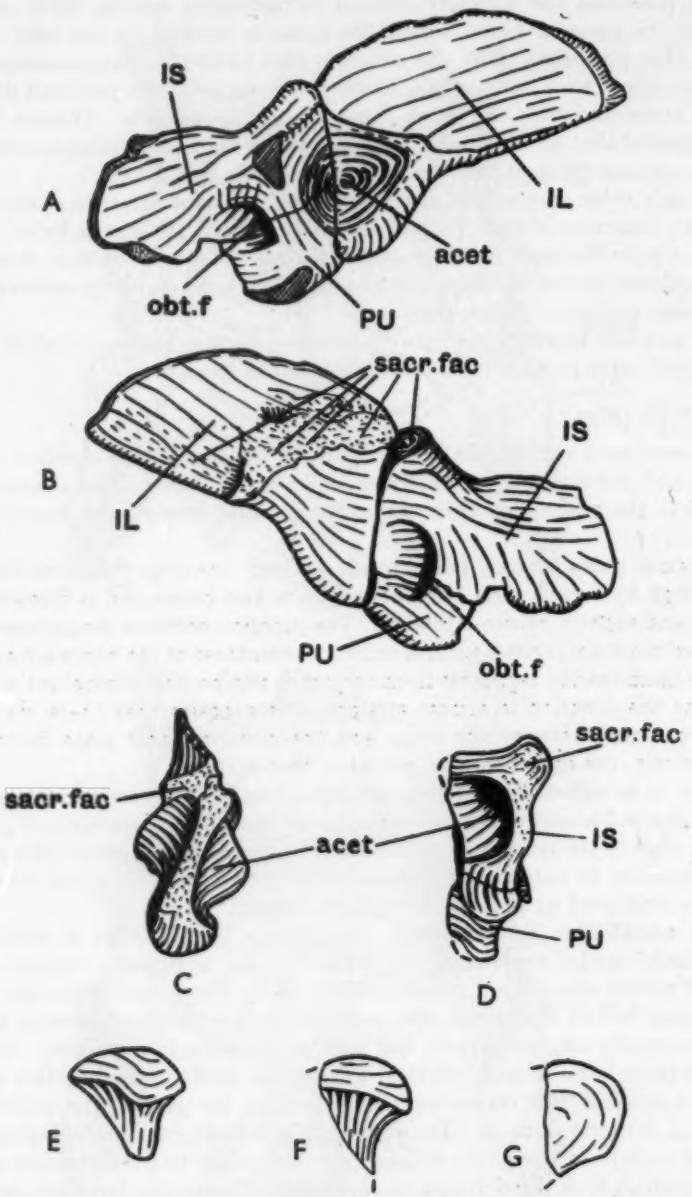

Fig. 15.—*Kingoria nowacki*, specimen no. 82, × 1. A, right half of pelvis in lateral view; B, right half of pelvis in medial view; C, posterior view of ilium; D, anterior view of ischium and pubis. E–G, portion of proximal end of right femur in E, medial view; F, anterior view; G, proximal view. acet, acetabulum; obt. f, obturator foramen; sacr. fac, facets for sacral vertebrae. For abbreviations of names of bones, see p. 367.

and the component attached to the blade of the ilium is known as the iliacus. The condition of the ilium suggests that this iliacus component may have attached to the lower part of the iliac blade in *Kingoria*, though such a mammalian character is quite unexpected in a Permian therapsid. The small preserved fragment of the femur (Fig. 15 E–G) is also advanced, as it appears to have had a fairly well-developed lateral head.

The unusual orientation of the pelvic girdle has the further result that a transverse connection between the two halves of the girdle would lie very close to the vertebral column, and it seems improbable that there was any bony symphysis in *Kingoria*. An examination of the literature shows that there is very little evidence for such a symphysis in any of the Dicynodontia. The only definite statement of its existence is in the semi-aquatic form *Lystrosaurus*; Watson (1912) states that the two ischia meet anteriorly in a short symphysis, but that posteriorly they diverge widely. Two dicynodont sacra were described by Broom (1925). In one, *Dicynodon sollasi ?*, he stated that there was little doubt that there had been a cartilaginous symphysis, and an examination of the original specimen, kindly lent by the University Museum, Oxford, supports this view. In the second specimen, *Dicynodon andrewsi ?*, Broom was of the opinion that there had been no such symphysis. Statements that there was apparently no pelvic symphysis have been made by von Huene (1931) for *Dicynodon kolbei ?* and by Pearson (1926 b) for *Kannemeyeria*, and von Huene (1935) stated that the two halves of the pelvic girdle were widely separated in *Stahleckeria*. No other described dicynodont remains give any evidence on this point. It thus appears possible that the absence of a bony symphysis between the two halves of the pelvis is normal in the Dicynodontia; there is no evidence as to whether a cartilaginous or ligamentous connection was commonly present.

THE TYMPANIC PROCESS

The most novel and interesting character found in the skull of *Kingoria nowacki* is the well-developed process extending posteriorly from the distal end of the paroccipital process, and which has already provisionally been referred to as the tympanic process. Its position, in the ventro-lateral portion of the occiput, is such that three possible functions suggest themselves: that it was concerned with the occipital musculature, with the jaw-opening musculature, or with the support of the tympanic membrane. These three possibilities will now be considered.

A. *The Occipital Musculature* (Fig. 16)

Some clues as to the siting of the occipital muscles have been obtained from the depressions and ridges that can be seen on the occiput itself. There are some scarred areas which apparently represent the regions of attachment of muscles but, because the character of impression that a muscle leaves on a bone varies according to whether the insertion of the muscle is fleshy or tendinous, it is impossible to come to any final conclusion. Where the muscle is fleshy, the bone may bear no indication of attachment; lack of surface

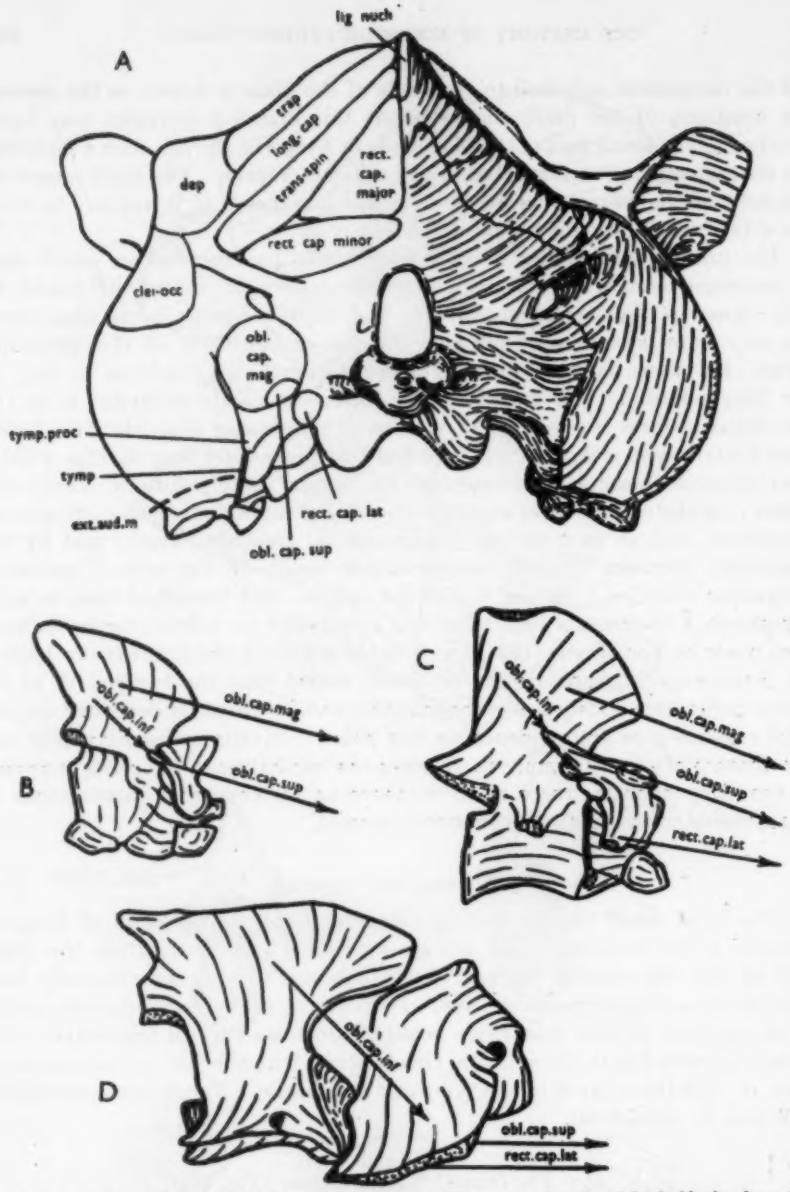

Fig. 16.—A, Occipital view of skull of *Kingoria nowacki*, ×1. On the right half, the form has been indicated by shading; on the left half, the posterior extension of the dorsal edge of the squamosal has been opened out dorsally, and the inferred positions of the occipital muscles have been indicated. B–D, atlas-axis complexes and courses of obliquus capitis and rectus capitis lateralis muscles in B, *Sphenodon*; C, *Ophiacodon* (muscles restored); D, *Felis*. Clei-occ, cleido-occipitalis muscle; dep, depressor mandibulae muscle; ext.aud. m, external auditory meatus; lig.nuch, ligamentum nuchae; long.cap, longissimus capitis muscle; obl.cap.inf, obliquus capitis inferior muscle; obl.cap.mag, obliquus capitis magnus muscle; obl.cap.sup, obliquus capitis superior muscle; rect.cap.lat, rectus capitis lateralis muscle; rect.cap.major, rectus capitis major muscle; rect.cap. minor, rectus capitis minor muscle; trans-spin, transverso-spinalis muscle; trap, trapezius muscle; tymp, tympanic membrane; tymp.proc, tympanic process.

marking in a given area does not therefore imply the absence of muscle insertions. It is necessary, therefore, to compare the muscle complexes of living reptiles and mammals and try to obtain some idea of what might be expected in an intermediate form such as *Kingoria*. Most muscles give little difficulty, and complications arise only in cases where mammals and reptiles have made divergent modifications. Since these changes in the muscle complex have been accompanied by changes in the morphology of the atlas-axis complex, a study of these vertebrae gave further direct evidence as to the condition in *Kingoria*.

Certain muscles which have constant positions in nearly all amniotes can be assumed to have been closely similar in position in *Kingoria*. These are as follows.

The most superficial muscle attached to the amniote skull is the trapezius, which runs from the occiput and the vertebral column to the pectoral girdle. Its insertion on the skull would be expected to be peripheral, dorsally from the ventral surface of the backwardly-projecting margin of the squamosal, and more ventro-laterally from the posterior surface of the ventral, occipital, wing of the squamosal. The more ventro-lateral part of the trapezius, running to the clavicle, tends to become a discrete muscle, the cleido-occipitalis. There is no direct evidence of the attachments of this muscle on either the skull or the girdle, but it seems quite likely that its origin was from the more lateral, posteriorly-directed, part of the clavicle, and its insertion on the dorsal part of the ventral, occipital, wing of the squamosal.

Normally, the muscle inserted under the trapezius in amniotes is the longissimus capitis, which originates from the transverse processes of the cervical vertebrae. These transverse processes are fairly stout in *Kingoria*, and the muscle probably inserted on the tabular and interparietal, along the dorso-lateral part of the occiput.

Below the longissimus capitis in amniotes is usually inserted the transverso-spinalis capitis (or semispinalis capitis) muscle, which originates from the bases of the spines and prezygapophyses of the cervical vertebrae. There is no direct evidence of this muscle on the cervical vertebrae, but it would be expected to be inserted dorso-laterally on the occiput, just under the longissimus capitis.

Also belonging to the transverso-spinalis system are the suboccipitalis muscles (obliquus capitis, and rectus capitis dorsalis and lateralis), which run between the occiput and the first two vertebrae. The rectus capitis dorsalis major in both reptiles and mammals originates from the dorsal edge of the axis spine and inserts on the dorsal part of the occiput, near the midline. Inserting just ventral to it is the rectus capitis dorsalis minor, whose origin is in *Varanus* (Nishi, 1916) from the anterior edge of the axis spine, in *Sphenodon* (Nishi, 1916) from the dorsal arch of the atlas in addition, in mammals from the latter alone; it seems probable that in *Kingoria* it originated from the large dorsal surfaces of the atlas arches.

The remaining rectus capitis lateralis and obliquus capitis muscles are not as readily susceptible to restoration, since the modern reptiles have modified the primitive amniote atlas and its associated musculature in a manner different from the modern mammals (Fig. 16, B-D).

Judging by *Seymouria* (White, 1939), the primitive amniote atlas was tripartite, consisting of an intercentrum and a pair of neural arches each with a neural spine and transverse process. In most later reptiles the atlas has remained tripartite, its neural spines and transverse processes are greatly reduced or lost, and movement of the head on the atlas-axis complex is accomplished by an obliquus capitis magnus muscle running from the axis spine to the occiput. In the mammals, however, the three elements of the atlas are co-ossified into a ring, within which the odontoid peg of the axis rotates, and the atlas possesses a very well-developed transverse process. Movement of the head on this atlas-axis complex is accomplished by an obliquus capitis inferior running from the axis spine to the dorsal surface of the atlas transverse process, and by an obliquus capitis superior and rectus capitis lateralis, both running from the ventral surface of the transverse process to the occiput.

Evans (1939) has attempted to derive the modern mammalian condition from that of a modern reptile. He suggests that the obliquus capitis inferior and superior have come into being because the atlas transverse process has enlarged and interpolated itself into the obliquus capitis magnus, subdividing it into these two muscles. However, he gives no clear reason for this interpolation, and it seems unnecessary to attempt to derive either of the modern conditions from the other. Instead, some idea of the manner in which the modern mammalian condition may have developed from that of the primitive amniote can be obtained from a study of the mammal-like reptiles.

A study of this group suggests that the paired neural spines of the atlas, as well as its transverse processes, were retained in the line of evolution which led to the mammals. In *Ophiacodon* and *Dimetrodon*, Romer & Price (1940) mention and figure a backwardly-directed spine external to the atlas postzygapophysis, and this region of the atlas also shows a projection in *Kingoria* (Fig. 7), in which it is stouter and more laterally directed than in the above-mentioned pelycosaurs. Such a structure is also present in gorgonopsids, being visible in an unidentified gorgonopsid in Parrington's collection (no. FRP 17), and in a figure of the cervical vertebrae of *Prorubidgea* (Brink & Kitching, 1954). In the cynodonts, Brink (1956) has figured the atlas-axis of *Diademodon* and restored a similar structure, though it is not present in the specimen of *Galesaurus* described by Parrington (1934).

The identification of this process as the neural spine would explain the presence of the obliquus capitis superior and inferior, since they would originally have been part of the normal series of interspinalis muscles which connect the neural spines of the more posterior vertebrae. In order to arrive at the mammalian condition, it is only necessary to suggest a fusion of the atlas neural spine and transverse process. Such a change is very likely to have occurred if the muscles, and thus the bony processes themselves, became larger. When the atlas had attained the unitary ring-like structure found in mammals, such an enlargement is likely to have taken place in order to take advantage of the extensive rotatory movements that this structure permits at the cranio-vertebral joint, and the enlargement of these muscles would presumably have been accompanied by the reduction of the reptilian obliquus capitis magnus muscle, the additional presence of which would no longer be necessary. The

rectus capitis lateralis, on this interpretation, represents part of the normal series of muscles which connect the transverse processes of successive vertebrae.

It thus seems likely that a primitive reptile would have had all three obliquus capitis muscles (magnus, superior and inferior). This would also be expected in a Permian reptile such as *Kingoria*, and the small size of the atlas neural spine certainly suggests that the obliquus capitis superior and inferior were not the only muscles responsible for movement of the skull on the atlas-axis complex. An obliquus capitis magnus muscle was probably also present and would have originated, in the usual manner, from the large axis spine. Its insertion was probably in the well-marked hollow on the occiput ventral to the post-temporal fossa and dorsal to the tympanic process, and the skull of *Kingoria* shows marks of muscle-insertion in this area. Such an insertion of this muscle, on the paroccipital process, occurs in both *Varanus* and *Sphenodon* (Nishi, 1916). The obliquus capitis magnus would thus run close by the atlas neural spine; the obliquus capitis superior would be running from this structure to the occiput and, since the occiput shows no trace of a separate insertion of the latter muscle, it seems quite possible that it inserted close to the obliquus capitis magnus.

Though the above reconstruction is inevitably somewhat tentative, it fits all the facts known to the writer and also provides a functional transition between the primitive reptilian and the mammalian conditions. As thus restored, the occipital musculature does not show any association with the tympanic process. The only occipital muscle which could reasonably be suspected of having been inserted on this process is the rectus capitis lateralis, which originates from the transverse process of the atlas. However, insertion on such a posterior projection from the occiput would significantly reduce the length, and so the range of action, of the muscle. Conversely, it seems unlikely that the tympanic process represents the point of insertion of a ligament restricting movement between the atlas and the occiput, since there are no signs of tendinous insertion on the tympanic process, and the atlas transverse process is larger than would be expected if it were merely the point of origin of a tendon.

B. *The Jaw Musculature*

The jaw muscles which are generally agreed to be present in the Reptilia are the capiti-mandibularis muscle mass and the pterygoideus muscles. The former is usually considered to be divided into temporalis and masseter components, though various writers have stated that it is often difficult to separate the two components completely (e.g. Adams, 1919; Becht, 1953).

The temporalis muscle probably originated from a large part of the medial and posterior walls of the temporal vacuity, and possibly also lateral to the root of the zygomatic arch. Part of its insertion is probably indicated by the strong wing on the lateral surface of the dentary, and the more medial portion presumably inserted on the inner surface of the mandible and into the meckelian fossa.

Parrington (1955) has suggested that the masseter in synapsids ran from the anterior portion of the zygomatic arch to the reflected lamina of the angular.

Such a course in the Dicynodontia is supported by the following features. Firstly, in *Stahleckeria* (von Huene, 1935), in the endothiodonts (Broom, 1921; 1932) and in various species of *Aulacephalodon* (Broom, 1932, 1936, 1941) there is a prominent ventrally or postero-ventrally directed knob under the postero-lateral corner of the orbit. A similar knob is found in the cynodonts *Cynognathus*, *Diademodon* and *Trirachodon*, and Parrington (1955) has suggested that it gave attachment to the masseter. Secondly, if the masseter of *Kingoria* originated from such a position, i.e. from the ventral surface of the junction of the zygomatic arch and the maxilla, its postero-ventral course to the reflected lamina would account for the abrupt manner in which the enlargement of the dorsal surface of the dentary for the attachment of the temporalis muscle is terminated posteriorly. Finally, if the courses here suggested for the temporalis and masseter muscles are correct, the resulting large angle between the two muscles would be well suited to producing the antero-posterior movement of the lower jaw suggested by Watson (1948).

The pterygoideus musculature of reptiles is divided into two portions (Adams, 1919). The anterior portion arises from the pterygoid and palatine region, and wraps around the ventral edge of the prearticular to insert on its outer face. The posterior portion arises from the pterygoid, epipterygoid and prootic regions, and inserts on the inner side of the mandible.

Following this, it seems likely that in *Kingoria* the position of insertion of the posterior pterygoideus is indicated by the marked scar found under the inner articular condyle, and that the muscle probably ran antero-dorsally onto the anterior face of the prootic. Such a course would also explain the way in which the inner articular condyle is undercut ventrally so that it projects as a medial wing from the body of the articular bone (Fig. 6E).

The anterior pterygoideus of *Kingoria* probably originated in normal fashion from the dorsal and lateral surfaces of the body of the pterygoid and ran postero-laterally to wrap around the posterior part of the jaw, having insertions on the outer side of the jaw under the reflected lamina, which Parrington (1955) believes was developed to provide an insertion for the masseter without restricting the anterior pterygoideus muscle. (A very similar structure is to be seen at the posterior end of the lower jaw of the modern rodent *Dasyprocta*, there being an outer rather thin sheet of bone to which the masseter is attached, and an inner, more solid, ridge of bone round which the pterygoideus is inserted). The posterior part of this anterior pterygoideus muscle is probably responsible for the very marked hollow on the anterior face of the retro-articular process; the fibres of this part of the muscle probably ran dorso-medially to an origin on the anterior portion and root of the quadrate ramus of the pterygoid. If this course is correct, those fibres which were attached to the anterior face of the retro-articular process, on the outer side of the mandible, would have at first to run medially. The necessity for providing a clear medial passage for these fibres may explain the manner in which the retro-articular process is sharply delimited anteriorly, instead of merging gradually into the ventral surface of the jaw ramus, for the latter would seem to be a mechanically stronger condition. It may be noted that a similar free medial access to the anterior face of the retro-articular process is still present even when the lower end of

the retro-articular process is directed anteriorly. This condition is found in the dicynodont *Emydochampsa oweni* (Broili & Schröder, 1936a) and in some gorgonopsids, and in such forms the retro-articular process is L-shaped; again, this condition is apparently unsatisfactory from a mechanical point of view, for it would seem that greater strength would have been provided if the angle between the two portions of the retro-articular process had been consolidated. The above interpretation of the anterior pterygoideus muscle would also to some extent reconcile the opinions of Watson and Parrington. Watson (1948) held that the apparent retro-articular process of later synapsids was in reality a process for part of the pterygoideus musculature (though he called this part the posterior pterygoideus), the retro-articular process and depressor mandibulae muscle having been lost; Parrington (1955) has put forward a strong case for the identity of this process with the retro-articular process of pelycosaurs. Parrington's identification of the ventrally directed process as the retro-articular process would seem to be confirmed by the clear traces of muscle insertion found on its posterior surface in *Kingoria* but, if the above interpretation is correct, it appears possible that the same process gave attachment to the depressor mandibulae muscle posteriorly and to the anterior pterygoideus muscle anteriorly.

Several factors make it seem likely that the origin of the depressor mandibulae muscle was from the posterior extension of the dorsal edge of the squamosal. Firstly, the antero-posterior alignment of the condyles on both upper and lower jaws suggests that the origin of the depressor mandibulae lay directly above its insertion so that the action lay in the plane of movement of the lower jaw. Secondly, the origin would be expected to lie some distance from the retro-articular process, since the movement of the jaws which could be produced by the contraction of a short muscle might not be sufficient to give an adequate gape. It should be noted here that the extensive antero-posterior movements of the lower jaw which are indicated by its disparity in length compared with the upper jaw, and also by the character of the condyles, and which have been suggested by Watson (1948), mean that the depressor mandibulae must be of considerable length if it is to allow these movements to take place. Finally, if the depressor mandibulae did run directly upwards from the retro-articular process, the most lateral part of the posterior extension of the dorsal edge of the squamosal provides a ventrally-directed surface well suited for its attachment. An origin from such a general region, high up on the occiput, is found in most modern reptiles, though this region is in such forms more usually occupied by the parietal than by the squamosal.

The above identification of the depressor mandibulae muscle does not in itself preclude the additional presence of muscles equivalent to the mammalian digastric. Furthermore, the process provisionally named the tympanic process lies in the region in which there is in mammals a process for the attachment of the digastric, the posterior belly of the muscle originating from a mastoid process of the periotic or from a paramastoid process of the occipital bone. In either case, the process is directed ventrally or ventrally and somewhat posteriorly, and the level of the jaw articulation is considerably more dorsal and anterior. The digastric and other muscles attached to the hyoid apparatus

are used either to open the jaws or to move the hyoid during swallowing. In *Kingoria*, however, the tympanic process is directed posteriorly and only slightly ventrally; moreover, it is dorsal and just posterior to the jaw condyle. Thus a muscle running from it to the hyoid, and serving to aid in opening the jaw, would have to run antero-ventrally around the middle-ear region. Hence, in terms of muscle effectiveness, the attachment of such a muscle on the tympanic process would be no more advantageous than would be a more ventral origin, e.g. on the basioccipital tubera. In addition, the character of the tympanic process does not suggest that it served for muscle attachment; it is too small to form a basis for a fleshy attachment, and its smooth surface makes it unlikely that a tendon originated from it. These factors thus do not support the hypothesis that there was a functional digastric system attached to the tympanic process in *Kingoria*; this conclusion is strengthened by the apparent presence of a well-developed depressor mandibulae muscle.

Crompton (1955b) has shown that that process of the paroccipital in scaloposaurid therocephalians which Watson (1931) named the " mastoid " process was probably extended laterally by cartilage so as to articulate kinetically with the squamosal; its function was thus apparently not for muscular attachment.

From the above discussion it appears that the jaw musculature of *Kingoria* was typically reptilian, possessing a depressor mandibulae muscle but no digastric muscle. Due to the more restricted nature of the movements which take place, and the correspondingly simpler character of the musculature, and due also to the greater amount of evidence afforded by the marking and relief of the bones, it has been possible to restore the jaw musculature with a greater degree of confidence than was possible in the case of the occipital musculature. Like the latter, the restored jaw musculature does not reveal any feature which is likely to have been responsible for the development of the tympanic process.

C. *The Auditory Region*

The presence or absence of a tympanum in the extinct reptiles is at present a subject of major controversy. Watson (1948, 1953, 1954, 1957) has maintained that the tympanum was absent in the captorhinomorph cotylosaurs and the more primitive synapsids, while Parrington (1955, 1958) has disputed this. Watson bases his theory on two main points: the lack of an obvious otic notch and the massive nature of the stapes. *Kingoria* provides evidence on both these points.

The tympanic process, together with the posterior extension of the inner quadrate condyle, produces a conformation well suited to the support of a tympanic membrane, and it has already been shown that alternative explanations appear to be inadequate to account for the form of this region. A tympanum in this position would necessitate the presence of a short external auditory meatus. A possible course for this is indicated by a notch in the lateral edge of the occiput just above the quadrate. This notch is formed by an inward and forward deviation of the quadratojugal, which forms the edge of

the occiput in this region. It is most clearly visible in lateral and postero-lateral views (Figs. 3A, 17A), and it is suggested that this notch may mark the position of an external auditory meatus running outwards and forwards.

As already mentioned, a clear muscle-scar on the posterior side of the retro-articular process shows that a depressor mandibulae muscle was present. This muscle would have formed the posterior border to the proximal part of the external auditory meatus (and perhaps also of the tympanum itself, as in

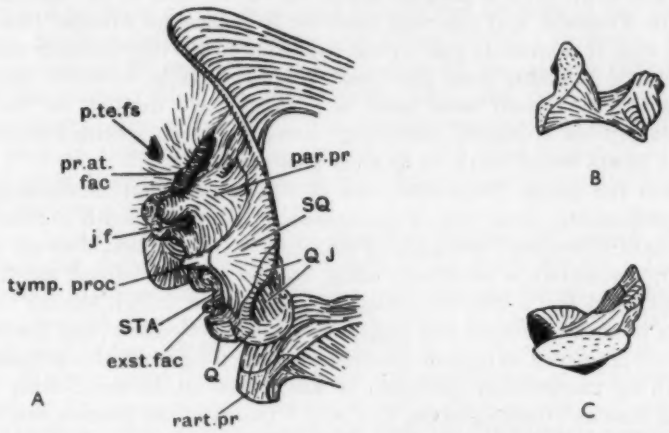

Fig. 17.—A, *Kingoria nowacki*, specimen no. 84. Postero-lateral view of right posterior quadrant of skull and posterior end of right ramus of lower jaw, × 1. B, posterior and C, distal views of left stapes of unidentified dicynodont, specimen no. 39, × 1. exst. fac, facet for extrastapes; j.f, jugular foramen; par. pr, paroccipital process of opisthotic; pr. at. fac, facet for proatlas; p. te. fs, post-temporal fossa; rart. pr, retro-articular process; tymp. proc, tympanic process. For abbreviations of names of bones, see p. 367.

some modern reptiles). It would thus interfere least with the auditory apparatus when the jaw was in its most posterior position, and the associated articular regions of upper and lower jaws in a large unidentified dicynodont (FRP 103) show a marked depression on the dorsal surface of the lower jaw immediately in front of the articular surface. The articular surface of the quadrate fits accurately into this depression, and it seems possible that the lower jaw, when not being used for feeding, was moved back until the quadrate slipped into this depression, the depressor mandibulae muscle being then held well clear of the auditory region.

The stapes of *Kingoria* is certainly a fairly broad bone in dorsal or ventral view, but in anterior or posterior view it is fairly thin. It has also been greatly shortened (and thus lightened) by bringing the fenestra ovalis towards the tympanic region by the development of basisphenoid tubera; this feature itself suggests that the weight and, by inference, the movement of the stapes was important—though the loss of the stapedial foramen in many dicynodonts is rather surprising. The expanded footplate of the stapes rests quite loosely in the fenestra ovalis, and is composed of spongy bone, thus further lightening the stapes. The stapes lies between the tubera and the quadrate, but is not

held tightly in place—indeed, in many specimens of dicynodonts it has dropped out. Additional evidence of the possibility of the stapes having functioned as a sound-transmitting structure lies in the presence of a small facet on its postero-lateral corner; this possibly marks the point of attachment of an extra-stapedial cartilage which ran to the tympanic membrane. In a larger dicynodont skull (FRP 39, possibly *Dicynodon huenei*) this part of the stapes bears a large process directed postero-dorsally (Fig. 17 B & C).

The above provides a possible theory as to the structures concerned with hearing in *Kingoria*, and one may next try to determine whether there is any evidence that it represents the typical condition in the dicynodonts as a whole. The evidence available from previously prepared skulls, in which mechanical methods of preparation were used, is unfortunately limited, as the slender tympanic process is readily destroyed; however, some specimens show clear breakage facets which mark its original position.

Within the genus *Dicynodon*, one of the earliest and smallest species is *D. pseudojouberti*, from the *Tapinocephalus* Zone of South Africa. Some specimens of this species were kindly provided by the British Museum (Natural History); the matrix is extremely hard, but the occiput of one specimen was largely exposed and a distinct tympanic process was found, similar to that of *Kingoria* in both character and position. *D. bathyrhynchus* (von Huene, 1942) has a well-preserved tympanic process 12 mm. long, and the process is also visible in an unidentified specimen of *Dicynodon* sp. in the British Museum (Natural History) (catalogue no. R 3745). Traces of the process can be found in *D. njalilus* and *D. locusticeps* (von Huene, 1942), and in *D. haughtonianus* (von Huene, 1931). Such a process has also been both described and figured in the Russian form *D. amalitzkii* (Sushkin, 1926) and is figured in the Chinese *D. sinkianensis* (Yuan & Young, 1934).

In other dicynodont genera, the type specimen of *Oudenodon bainii* in the British Museum (Natural History) (catalogue no. 36232) shows a clear breakage facet where the tympanic process might be expected; a similar facet can be seen in *Tropidostoma microtrema* (Seeley, 1889, plate 11) and the process itself can be seen in another specimen of the same genus (Seeley, 1889, plate 12).

Conditions in the three large Triassic genera are inconclusive. In *Kannemeyeria*, Haughton (1915) mentions that " the posterior corner of the paroccipital is prolonged to form a bluntly pointed process "; this can also be seen in Pearson's (1924 a) figures of this region in *K. erithrea*, in which it appears to be a low mound. In the South American genus *Stahleckeria* the distal end of the paroccipital process bears a strong low mound, and the stapes has a roughened area at its postero-distal corner which may mark the point of attachment of a cartilaginous extra-stapes. In the North American genus *Placerias*, Camp & Welles (1956) state that there is no posterior ridge or process on the paroccipital process. They figure and mention an extra-stapedial facet on the stapes and a groove running laterally along the back of the quadrate. They state, without further discussion (p. 275) that " it seems unlikely that a tympanum would have been buried in the jaw muscles at any point median to the margin of the squamosal ". The stapes also possesses a great proximo-ventral boss adjacent to the footplate, which Camp & Welles interpret as an attachment of one of

the sub-cervical muscles, developed powerfully to rake the muzzle downward and backward while grubbing in the ground. However, the stapes is not fused to either the tubera or the quadrate.

Finally, there are two genera in which no trace of the tympanic process could be found. Skulls of the semi-aquatic genus *Lystrosaurus* which have been prepared with acid show that a small posterior area of the distal end of the paroccipital process lacks a hard perichondral bone layer, but there is no other hint of any modification which might be associated with a tympanum. In *Cistecephalus* no trace of the tympanic process can be seen in the very clear figures of Broili & Schröder (1935 a) and Brink (1950). However, both the strong box-like skull and the peculiar nature of the manus (Brink, 1952) suggest that *Cistecephalus* was a burrowing form, and degenerative changes in the auditory apparatus of modern reptiles are most common in forms leading such an existence, presumably because the head is usually in contact with the ground, so that it is possible for vibrations to be conducted directly through the bones of the skull.

Only a small proportion of the described dicynodont genera (of which there are about sixty) have been mentioned in the above survey. Though an examination has been made of all the available specimens in the British Museum (Natural History), and in the Museums in Cambridge, Oxford and Tübingen, and in the private collections of Dr F. R. Parrington and Professor D. M. S. Watson, many of the genera are not represented in European collections and, in any case, relatively few specimens show a clear and undamaged occipital surface. The evidence available from the literature is equally scanty and naturally more difficult to assess. It is thus impossible to make any definite statement as to how far the structures found in *Kingoria* are typical of the dicynodonts as a whole. Enough evidence has been collected to make it appear likely that it was present in the rather ill-defined genus *Dicynodon*, and in *Oudenodon* and *Tropidostoma*. Some genera do not show these conditions; it would not seem to be unreasonable to suppose that in these cases either the great increase in size (*Kannemeyeria*, *Stahleckeria*, *Placerias*) or the unusual habitat (*Lystrosaurus*, *Cistecephalus*) have rendered unnecessary the retention of a special process to support the dorsal margin of the tympanum. *Dicynodon* itself is certainly a more primitive genus, and the presence of the tympanic process in an early (*Tapinocephalus* Zone) species of that genus makes it appear possible that it was a character possessed by the Dicynodontia as a whole. This would support the view of Parrington (1955, 1958) that a tympanic membrane was present and functional in the primitive synapsids.

THE POST-TEMPORAL FOSSA AND THE VEINS OF THE HEAD

Originating merely as a gap between the bones of the dorsal roof of the skull and the bones of the dorsal part of the occiput, the persistence of the post-temporal fossa in the majority of the tetrapods implies that it had some functional significance. Though in many fossil amphibia it is large and may have served for the origin of part of the neck musculature (Romer, 1941), its function in the reptiles appears to be as a passage for a blood vessel. This is supported by its small size in many reptiles and by the presence in some

fossils, including *Kingoria*, of well marked grooves running from its anterior opening. It is possible to identify this blood vessel as the vena capitis dorsalis, which in various modern reptiles (*Lacerta*, Bruner, 1907; *Sphenodon*, O'Donoghue, 1920) drains the occipital musculature and runs forwards through the region morphologically equivalent to the post-temporal fossa. The vena capitis dorsalis is joined from an anterior direction by a sinus-like vena parietalis; it then enters the cranium, between the parietal and the prootic, and joins the vena cerebralis media.

The deep groove on the anterior face of the prootic in *Kingoria* probably marks the course of the vena capitis dorsalis from the post-temporal fossa to its entry into the cranium at a notch in the anterior wall of the braincase (Fig. 3C, v. notch). There is no evidence of the presence or course of a vena parietalis in this dicynodont, but a more extensive system of grooves is found in the cynodonts. In *Diademodon* (Watson, 1911) there is a groove along or just above the junction of the parietal and epipterygoid. At about one centimetre behind the level of the pineal foramen this groove receives a large oval and backwardly directed foramen, which Watson states must lead into the brain cavity, and the internal opening of which he later found (Watson, 1913); the groove continues beyond the foramen and runs into the post-temporal fossa. The foramen which Watson mentions has also been found in several other genera of cynodonts. Comparison with the living forms suggests that the foramen is the point of entry of the vena capitis dorsalis into the braincase, and that the groove anterior to the foramen represents the vena parietalis.

Olson (1944) found a notch in the anterior border of the periotic, in a position similar to that of the notch which has above been considered to be the point of entry of the vena capitis dorsalis in *Kingoria*. He states that the notch is present in most of his serially-sectioned specimens, which include dicynodonts, therocephalians, gorgonopsids and cynodonts, and that it is commonly separated from the prootic incisure by an antero-dorsal process of the periotic. However, because the notch does not appear to be present in some forms, and because it is occupied by the epipterygoid in his cynodonts, Olson does not believe that it was traversed by a blood vessel. Instead he follows Price (1935), who suggested that a ledge on the anterior margin of the prootic in *Captorhinus* was the base for a cartilage supporting the orbitosphenoid elements, stating that a comparable shelf with such a function is found in modern iguanas. Olson interprets the antero-dorsal process in his therapsids as having had a similar function, and believes that the appearance of the dorsal incisure is merely incidental to the development of this structure.

However, in the iguanas the relatively large size of the orbit and its posterior position have led the supporting elements of the orbitosphenoid to come into relation with the anterior margin of the prootic. It seems inadvisable to homologise the resulting structural features with those found in these fossil reptiles, in which the orbit is much smaller and is situated very much further forwards relative to the braincase. The lack of an incisure in the cynodonts is not surprising since, as mentioned above, the entrance of the vena capitis dorsalis is through a foramen between the epipterygoid and the parietal, in a position more dorso-anterior than in the other therapsids, so that the vein

may well not have passed across the front border of the prootic. The exact course of the vein may well vary in the different therapsids, and this would lead to corresponding variations in the presence or depth of the incisure.

On the above evidence, it seems to the writer more reasonable to explain the incisure as being a result of the presence of a vena capitis dorsalis, than to account for it as being merely an incidental in the development of a structure bearing a cartilage supporting orbitosphenoid elements.

In addition to the grooves mentioned above, *Kingoria* shows some indications of a groove running downwards from the post-temporal fossa; in the cynodonts a similar groove runs into the pterygo-paroccipital foramen, and a further groove runs from this latter foramen forwards to the facialis foramen (Watson, 1911; Parrington, 1946 a). In *Diademodon*, at least, the whole system of grooves is covered by thin flanges from the surrounding bones (Watson, 1911).

Watson (1920) has suggested that the vena capitis lateralis passed through the pterygo-paroccipital foramen, then giving rise to one branch which passed through the post-temporal fossa, a second which passed up the dorsal groove along the junction of the parietal and prootic, and a third (presumably the continuation of the vena capitis lateralis) which ran dorsal to the meeting of the prootic and epipterygoid and passed through the trigeminus foramen between these two bones. However, the fact that the post-temporal fossa is occupied by a vein draining forwards makes some modification of this necessary. The post-temporal fossa and dorsal groove were presumably occupied by the vena capitis dorsalis; the vena capitis lateralis presumably ran from the pterygo-paroccipital foramen into the trigeminus foramen. The groove between the post-temporal fossa and the pterygo-paroccipital foramen was probably occupied by a vein joining the vena capitis lateralis and the vena capitis dorsalis, and providing an alternative method of drainage—a common feature in the veins of the head. The groove for this vein is more marked in the cynodonts, where the post-temporal fossa and the pterygo-paroccipital foramen are closer together, and it is possible that in the cynodonts this became the only drainage for the vena capitis dorsalis. This would explain the lack, in *Cynognathus crateronotus* (Seeley, 1895 b) of a foramen at the antero-dorsal end of the groove for the vena capitis dorsalis, the direction of flow in this part of the vein having reversed so that it runs posteriorly, meeting the main inflow through the post-temporal fossa and continuing downwards to meet the vena capitis lateralis near the pterygo-paroccipital foramen.

THE MODE OF LIFE OF *KINGORIA*

The great abundance of remains of the Dicynodontia suggests that the group was in general herbivorous. In the majority the dentition is reduced and food must have been gathered by a scissor-like action of the sharp cutting edges on the jaw margins, which Owen long ago suggested were sheathed by horn during life. However, this method could not have been used by *Kingoria*, since these edges are not sharp and because the lower jaw tapers to a rounded, blunt, slightly bilobed point whose outline does not conform to that of the margins of the palate. Furthermore, if the articular surfaces of the articular

and quadrate of *Kingoria* are placed in contact and the lower jaw is progressively closed, it is found that, so long as the articular surfaces remain in contact, it is impossible for the anterior end of the lower jaw to touch the palate, since the more posterior part of the dentary meets the ectopterygoid region of the palate before any more anterior meeting can take place. It is possible that a meeting was achieved by an extensive separation between the quadrate and articular condyles, but the necessity for such a meeting in the absence of cutting edges on the jaws is not apparent. Alternatively, it is possible that the outline of the bony jaws is not representative of the outline of the horn which covered them, and that sharp edges on the horn of the lower jaw may have cut against the edge of the upper jaw. However, study of the horny beaks of modern Chelonia and birds shows that, wherever a sharp cutting edge is present, the horn layer is thin and the underlying bone gives an accurate picture of the nature of the beak. It is only when it is forming a crushing surface that the horny layer becomes thick and conforms less closely to the relief of the underlying bone. Thus it seems unlikely that the lower jaw of *Kingoria* possessed a cutting edge and, furthermore, the curved, tapering shape of the anterior end of the lower jaw does not provide the flattened area which is normally found in those forms (e.g. mollusc-eating animals) in which the jaws are used for crushing.

The shape of the anterior end of the lower jaw could be explained by two possible modes of life. Firstly, it is possible that the blunt point was used for grubbing in the ground for roots; this mode of life might be expected to have led to modifications of the limbs and feet, but these are unfortunately missing. Secondly, it is possible that the narrowing of the anterior end of the lower jaw was to give freedom of action to a very mobile tongue, which the animal used to browse on the surface vegetation. The strong jaw musculature, which is indicated by the development of the lateral wing on the dentary, makes the first explanation somewhat more probable, but the problem remains as to how the food which had been excavated was broken up before swallowing. However, since little is known of the flora of the African Permian, and thus of the possible plants upon which *Kingoria* may have fed, it is impossible to carry useful discussion beyond this point.

THE HOMOTAXY OF THE LOWER BONE-BEARING SERIES AT KINGORI

Haughton (1932) and von Huene (1942) have concluded, from a study of the fauna of the Lower Bone-Bearing Series, that the Series includes levels homotaxial with both the *Endothiodon* and the *Cistecephalus* Zones of South Africa. Unfortunately, the Lower Bone-Bearing Series shows no sign of a division between these zones. Nowack (1937) has given a detailed description of profiles through the Series at three localities, and he states that they show important differences from one another, and that it is not possible to make an exact correlation between the various strata at each locality. Despite this, study of the stratification of the fauna at one locality should provide evidence of the time-range of the Series. Most of the vertebrate fauna was collected at Kingori, and Nowack's table (1937, p. 403) shows at what level the different

specimens were found. By referring to von Huene's descriptions (1942, 1944, 1950) of these specimens, it is possible to build up a fauna-list for each level.

The presence of *Cistecephalus* itself at a level near the top of the profile confirms that part of the Series is homotaxial with the *Cistecephalus* Zone, but the character of the lower levels does not provide confirmation of the existence of any level homotaxial with the *Endothiodon* Zone. On the contrary, the lowest level contains *Dicynodon huenei**, itself of *Cistecephalus* Zone affinities, and which occurs at a slightly higher level with *Pelanomodon*, a dicynodont genus which is definitely known from the *Cistecephalus* Zone. *D. huenei* also occurs above *Kingoria*, the only South African species of which comes from the *Cistecephalus* Zone. The rest of the fauna of Kingori is similarly indicative of affinities with the *Cistecephalus* Zone, with two exceptions—*Cryptocynodon* and *Neomegacyclops*.

The horizon of the small dicynodont *Cryptocynodon parringtoni* (von Huene, 1942) is uncertain, since it is not indicated on Nowack's (1937) table or map. von Huene (1942) states that, judging by the reddish colour of the matrix, the skull probably came from the lowest zone, slightly more than 30 m. above the Ruhuhu Beds. The genus *Cryptocynodon* was founded by Seeley (1895 a) for the badly preserved anterior end of a skull, it being characterised by having a row of post-canine teeth placed behind and internal to the canine; its horizon is unknown. Broili & Schröder (1935 b) have provisionally placed another specimen in this genus, without assigning it a trivial name; it comes from the uppermost *Endothiodon* Zone. Janensch (1952) has described another form, which he states is probably from the Upper *Endothiodon* Zone and which he provisionally names *Cryptocynodon ? schroederi*, though he does not indicate that the post-canine teeth are internal to the canine; he states that the relationship of this form is uncertain. There is thus some evidence that the genus *Cryptocynodon* occurs in the *Endothiodon* Zone, but it is quite possible that it also extends up into the Lower *Cistecephalus* Zone. von Huene (1942, p. 184) states that in South Africa the dicynodonts possessing post-canine teeth are characteristic of the *Endothiodon* Zone, but this is incorrect. Of the smaller genera of this group (i.e. those whose skulls are less than 130 mm. long), four come from the *Tapinocephalus* Zone, one from this Zone or the *Endothiodon* Zone, six from the *Endothiodon* Zone, two are found in both the *Endothiodon* and the *Cistecephalus* Zones, and four come from the *Cistecephalus* Zone.

A species of *Neomegacyclops* from Kingori has been described by Boonstra (1953). Three of the four known species of this genus are from Tanganyika, but the genus is founded on the South African species *N. whaitsi* which Haughton & Brink, in their recent bibliography (1954), list as from the *Endothiodon* Zone. However, the type specimen was originally stated to be from the *Cistecephalus* Zone (Haughton, 1917). Furthermore, all definite evidence as to the horizons of the different genera of large tuskless dicynodonts which

* The original ascription (Haughton, 1932) of this form to *Dicynodon* is here retained; von Huene (1942) referred it to *Platypodosaurus*, but *Dicynodon huenei* differs from it in its short and deep skull (that of von Huene's *Platypodosaurus magnus* being very elongate and flattened), in its lack of a pineal boss and of elongate caniniform processes, and in possessing canine tusks.

bear a pineal boss is that they are from the *Cistecephalus* Zone. *Kitchingia* is from the *Cistecephalus* Zone; it was originally separated (Broom & George, 1950) from *Neomegacyclops* because it appeared to lack a preparietal, but this bone was later found (Brink, in addendum to same paper). It is similar to *Neomegacyclops* in having a wide exposure of the parietal in the intertemporal bar, whereas the postorbitals meet above them in the midline in the other forms which have a pineal boss. It therefore seems reasonable, the original ground for separating the two genera having proved incorrect, to refer *Kitchingia planifrons* (the only species) to the genus *Neomegacyclops* as *Neomegacyclops planifrons* (Broom & George). Of the other related genera, *Rhachiocephalus* and *Platycyclops* are known from the *Cistecephalus* Zone of South Africa; *Platypodosaurus magnus* (of von Huene, 1942) comes from Kingori from a level which contains *Cistecephalus*; and the horizons of *Pelorocyclops* and *Eocyclops* are not known.

Thus the original ascription of the type specimen of *Neomegacyclops*, the horizon of another species which was formerly incorrectly placed in a different genus, and the horizons of other related genera, all indicate that *Neomegacyclops* is a form from the *Cistecephalus* Zone or homotaxial horizons.

There is thus no firm evidence for the presence at Kingori of a level homotaxial with the *Endothiodon* Zone of South Africa. However, the presence of such a level elsewhere in the Ruhuhu area is shown by the occurrence of endothiodont remains at Usili (Haughton, 1932) and Ruanda (Parrington, in discussion at end of Haughton, 1932). It therefore seems that the *Endothiodon* Zone is represented at Usili but not at Kingori, and it may be relevant to note that a basal bone-bearing sandstone layer is found at Usili but not at Kingori (Nowack, 1937). However, the horizon of the endothiodont remains is unknown.

SUMMARY

1. A new genus of dicynodont, *Kingoria*, is defined and described. The genotype is *Kingoria nowacki* (von Huene) from the Lower Bone-Bearing Series of South-west Tanganyika, and another species, *Kingoria galecephala* (Broom & Robinson), comes from the *Cistecephalus* Zone of South Africa.

2. The occiput of *Kingoria nowacki* bears a posteriorly-directed process which has been named the tympanic process, since it probably held the dorsal edge of the tympanum. This process may be a normal characteristic of the Dicynodontia, since it is present in the *Tapinocephalus* Zone form *Dicynodon pseudojouberti* and in some other genera.

3. The occipital musculature of *Kingoria* is restored and a new theory is suggested as to the evolution of the muscles which run between the atlas-axis complex and the occiput in mammals.

4. The jaw musculature of *Kingoria* is restored and the differing interpretations of Watson and Parrington as to the identity of the ventrally directed process of the articular bone are reconciled.

5. The course of the vena capitis dorsalis through the post-temporal fossa and into the braincase in *Kingoria* is identified, and the functions of the extensive system of venous grooves in the cynodont skull are discussed.

6. *Kingoria* has six cervical vertebrae; this is the first dicynodont in which firm evidence of the number of cervical vertebrae has been found.

7. In the dorsal vertebrae of *Kingoria* the upper part of the transverse process is free from the attachment of the tubercular head of the rib and forms a blunt, rounded, dorso-laterally directed process, which is called a metapophysis. This process, which was presumably for muscular attachment, may be normal in the Dicynodontia.

8. The cervical and anterior dorsal ribs of *Kingoria* are double-headed, while the more posterior dorsal ribs are single-headed and appear to attach to the side of the centrum.

9. There is no cleithrum in *Kingoria*. This bone has been reported only in one unidentified dicynodont, in *Cistecephalus* and in *Kannemeyeria*, and its absence may be a more general feature in the Dicynodontia than had been thought.

10. The scapula of *Kingoria* bears a prominent spine along its antero-external edge, as in monotremes. A further mammalian character, the presence of an iliacus muscle, is suggested by markings on the blade of the ilium.

11. The ischium and pubis of *Kingoria* are posterior to the ilium, which does not extend behind the level of the acetabulum. The fourth sacral rib touches the ischium.

12. It is unlikely that there could have been any bony connection between the two halves of the pelvis of *Kingoria*; this condition may be usual in the Dicynodontia.

13. The mode of life of *Kingoria* is uncertain; it was probably herbivorous, and may have rooted in the ground for its food.

14. Study of the fauna from the type-locality of *Kingoria* shows that the whole of the Lower Bone-Bearing Series there is probably equivalent to the *Cistecephalus* Zone of South Africa, though a level equivalent to the *Endothiodon* Zone appears to be present at some other localities in the Ruhuhu area.

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KEY TO ABBREVIATIONS OF NAMES OF BONES IN THE FIGURES

A	Angular	PMX	Premaxilla
ART	Articular	PO	Postorbital
BO	Basioccipital	PP	Preparietal
CL	Clavicle	PR.ART	Prearticular
CO	Coracoid	PRF	Prefrontal
D	Dentary	PRO	Prootic
ECT	Ectopterygoid	PSP	Parasphenoid-basisphenoid complex
EPT	Epipterygoid		
F	Frontal	PT	Pterygoid
ICL	Interclavicle	PU	Pubis
IL	Ilium	Q	Quadrate
IP	Interparietal	QJ	Quadratojugal
IS	Ischium	SA	Surangular
J	Jugal	SC	Scapula
L	Lacrimal	SMX	Septomaxilla
MX	Maxilla	SO	Supraoccipital
N	Nasal	SPL	Splenial
OP	Opisthotic	SQ	Squamosal
P	Parietal	STA	Stapes
PAL	Palatine	STM	Sternum
PCO	Precoracoid	T	Tabular
		V	Vomer

ON *TROCHETA BYKOWSKII* GEDROYĆ, 1913, A LEECH NEW TO THE BRITISH FAUNA, WITH NOTES ON THE TAXONOMY AND ECOLOGY OF OTHER ERPOBDELLIDAE

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With an appendix by C. S. Woods

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(With 3 figures in the text)

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INTRODUCTION

In February 1957 the author received from Mr C. S. Woods of Queen's University, Belfast, some leeches from two areas in the neighbourhood of Belfast. Mr Woods pointed out that these fitted the description of *Trocheta subviridis* Dutrochet except for the fact that they had only two annuli separating the genital pores whereas *T. subviridis* has six to eight. By a remarkable coincidence some leeches of the same type were sent to the author in June 1957 having been collected in Windermere by Mr J. D. Allanby of the staff of the Freshwater Biological Association. The leeches from both sources agree with the description of *Trocheta bykowskii* Gedroyć, 1913, a species never before recorded for Britain.*

This leech was first described (Gedroyć, 1913) from spring-water in the Carpathians. In a subsequent paper (Gedroyć, 1916) it was placed in a new genus *Blanchardia*, distinguished from *Trocheta* by the fact that a typical somite consisted of eleven equal annuli instead of three wide and five narrow annuli. Pawlowski (1936) compared the annulation of *B. bykowskii* with that of *Trocheta subviridis* and with other species of *Trocheta* and showed that the difference emphasized by Gedroyć is not constant, and that the most

* Since sending this paper to press specimens of *T. bykowskii* have been obtained from the River Penk in Staffordshire, the River Thames at Reading, Berkshire, and the Braid Burn in Edinburgh.

that could be said was that there was a greater tendency for the wide annuli of *B. bykowskii* to become subdivided. He therefore proposed that the species *bykowskii* should revert to the genus *Trocheta*. Pawlowski (1938 a and b) subsequently collected *T. bykowskii* from the Polish East Carpathians and studied both its distribution in the field and its behaviour in the laboratory. He concluded that it is restricted to cold mountain streams, and that it colonizes reaches where no other leech can survive on account of the speed of the current. It manages to survive by spending a great deal of its time out of the water, under stones in damp places. It shares this habit with *Haemopis sanguisuga*, but in any given area it tends to occupy the headwaters of the stream, while *Haemopis* is found lower down.

Pawlowski (1949) referred to a specimen of *T. bykowskii* taken from the River Mur, in Austria, and commented that this was the first record from West of the Carpathians.

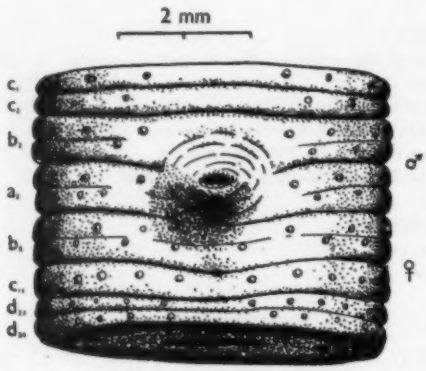

Fig. 1.—Ventral view of segment XII of a sexually mature specimen of *Trocheta bykowskii*. The annuli are labelled according to the system of Moore (1927).

Perret (1952 a) recorded *Trocheta bykowskii* from the Neuchatel region of Switzerland and found that it was confined to running, calcareous water, remarking that it was the only leech of the region which did not enter the lakes. Perret also described specimens from the municipal museum of Gênes. These leeches had been collected from three localities in Italy, and the number of rings between the genital pores varied from two-and-a-half to six. These leeches were all referred to *T. subviridis* but in this particular character there is clearly a gradation between the two species. Perret (1952 b) therefore proposed that there should be only one species, *T. subviridis* Dutrochet, with two subspecies *T. subviridis subviridis* and *T. subviridis bykowskii*.

Dresschner & Engel (1955) recorded *Trocheta bykowskii* from various localities in Holland and Belgium, and concluded that its normal habitat in these countries was " a medium now and then flooded by water which is a little brackish ". They also pointed out that the records by Verriest (1950) for *Trocheta subviridis* in Belgium and Holland really referred to *T. bykowskii*

and that a previously unidentified specimen in Leiden museum collected from a market garden in Leiden in 1925 is also *T. bykowskii*.

THE EXTERNAL CHARACTERS OF THE BRITISH *T. BYKOWSKII*

Regarding size, shape and annulation there is no constant difference between *T. bykowskii* and *T. subviridis*, to judge from the British material, although up to the present time no specimens of *T. bykowskii* have been discovered which are as large as the largest *T. subviridis* previously recorded (Mann, 1952). A segment in the mid-body region of a sexually mature specimen of *T. bykowskii* (Fig. 1) consists of two narrow annuli, followed by three wide annuli faintly subdivided by very shallow grooves, and finally three narrow annuli. Of the last group, the second and third are obviously formed by the subdivision of a wider annulus, but the first one is distinctive in being intermediate in width between a wide and a narrow annulus. In the terminology of Moore (1927) the formula for a segment is :—

$$c_1=c_2<b_3=a_2=b_5>c_{11}>d_{23}=d_{24}$$

The genital pores in all the specimens examined are separated by two large annuli, the male pore in the furrow $XIIb_2/a_2$, and the female pore in the furrow $XIIb_5/c_{11}$ (Fig. 1).

Large specimens with a clitellum have a reticulum of dark pigment on the dorsal surface, which may cover the whole area except for a row of small whitish spots running transversely across the centre of each annulus. These whitish spots, which are the segmental and annular receptor organs, are raised and give the dorsal surface a roughened appearance to the naked eye which is quite different from the appearance of *T. subviridis*. Smaller specimens have two dark parallel lines running longitudinally on the dorsal surface, as in *T. subviridis* and *Dina lineata*.

THE TAXONOMIC STATUS OF *TROCHETA BYKOWSKII*

The attempt by Gedroyć (1916) to justify the placing of *bykowskii* in a separate genus, *Blanchardia*, on the grounds that the arrangement of the annuli is distinctive, is in no way supported by the British material. Faint subdivision of the broad annuli has been observed in both *subviridis* and *bykowskii*, although rather more frequently in the latter species. We may also consider the merits of Perret's (1952 b) proposal that they should be regarded merely as distinct subspecies. The separation of the genital pores by two to three rings in *bykowskii* and by six to eight rings in *subviridis* has been found to be a constant difference in Poland, Switzerland, Austria, Holland, Belgium and Britain. The British material also shows a recognizable difference in colour and in surface texture in the fully grown forms. These differences are as great as those separating *Erpobdella octoculata* from *E. testacea*. Moreover, dissection of the British material has revealed a constant difference between the two species of *Trocheta* in the arrangement of the ovisacs. As may be seen in Fig. 2, the ovisacs, of *bykowskii* enclose three ganglia within the loop, being widely separated until they reach the anterior border of segment XVI, while those of *subviridis* enclose only one ganglion within the loop, and come together at the level of ganglion XIV. Most students of the group would

agree that there are sufficient differences to separate clearly the two forms as distinct species, and the existence of some specimens from Italy which show intergradation in the number of rings between the genital pores does not invalidate the distinction. Presumably these specimens are hybrids, and

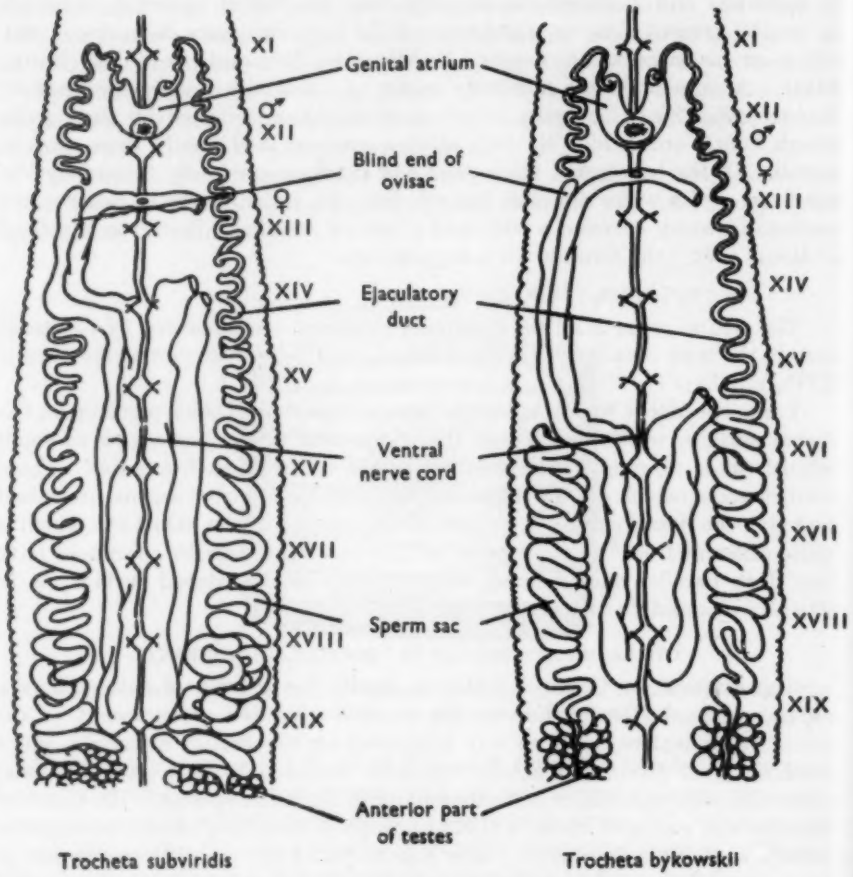

Fig. 2.—Diagrams showing part of the reproductive system of two species of *Trocheta* as seen when dissected from the ventral side.

occasional hybrid forms are well known in other groups, such as the freshwater fishes, where they are not regarded as a reason for merging the species which hybridize.

THE RELATION BETWEEN TROCHETA, DINA AND ERPOBDELLA

There are now five species of erpobdellid known in Britain : two species of *Trocheta* referred to above, two species of *Erpobdella*, *E. octoculata* (L.) and *E. testacea* (Savigny, 1820), and a species described in a previous paper (Mann,

1952) under the name *Dina lineata* (O. F. Müller, 1774). The relation between these merits further consideration in the light of two recent papers dealing with Erpobdellidae, by Moore (1951) and Pawlowski (1955). Moore, in describing a new species from Alaska which he called *Dina dubia* drew attention to the fact that of the six North American species which have been referred to *Dina*, two resemble *Erpobdella* in having the sperm duct thrown into a preatrial loop, while the remaining species lack the preatrial loop. He tentatively suggested that a way out of this difficulty would be to unite *Erpobdella* with *Dina* as a single genus with three subgenera.

Pawlowski (1955) followed up this suggestion in a paper dealing with records of *Dina* and *Erpobdella* from many parts of the world. He proposed that there should be one genus *Erpobdella* de Blainville, 1818, with the following three subgenera :

(1) Subgenus *Erpobdella* Pawlowski, 1955, in which the five annuli of a segment are subequal, or the b6 annulus is a little wider than the others but is never subdivided. The sperm ducts form preatrial loops reaching forward to about ganglion XI of the ventral nerve cord.

(2) Subgenus *Dina* Harant, 1929, in which the b6 annulus of a segment is wider than the others and divided by a shallow transverse groove. The sperm ducts form a preatrial loop reaching forward to ganglion XI.

(3) Subgenus *Mooreobdella* Pawlowski, 1955, in which the b6 annulus is subdivided, but the sperm ducts do not form a preatrial loop.

If Pawlowski's scheme is adopted, *Dina lineata* will be known as *Erpobdella* (*Dina*) *lineata*, *E. octoculata* and *E. testacea* will belong to the subgenus *Erpobdella*, and the subgenus *Mooreobdella* will have no representatives in the British fauna. However, for reasons given below, the author doubts the advisability of placing *lineata* in the genus *Erpobdella*. The two species of *Trocheta* resemble the other British erpobdellids in possessing preatrial loops in the sperm ducts. Moore (1927) included in his diagnosis of this genus the statement that the atrial cornua have a spiral turn. In the British material this has only occasionally been observed, and is therefore not a valid distinction.

Leech systematists have not made much use of the characters of the female reproductive system in their schemes of classification, but certain constant differences have been noted in British erpobdellids. The ovisacs take the form of two elongated tubes bent back on themselves. Their blind ends lie quite close to the female pore, and from here the sacs run backward for a few segments, then turn sharply forward and run to the female pore. (Figs. 2 and 3). When the eggs have all been discharged the ovisacs may not fill the space available to them in the body, but as the time for ovulation approaches the sacs become distended to the full extent of the coelomic spaces in which they lie. The posterior limit of the ovisacs in a sexually mature leech has been found to be reasonably constant for the species. In both species of *Trocheta* they reach to segment XIX, in *E. testacea* to XVIII, in *E. octoculata* to XVII and in *Dina lineata* to XV (Fig. 3). In *E. octoculata* the ovisacs are widely separated along their length, while in *E. testacea* and the two species of *Trocheta* they are separate for a few segments and then come together in the mid-ventral line and lie just above the nerve cord. In *Dina lineata* the

arrangement is quite different, since the ovisacs are bunched anteriorly. Thus, on the basis of the female organs *Dina lineata* stands apart from the rest, and the author considers it inappropriate to place *lineata* in the same genus as *octoculata* and *testacea* until more is known about the female organs of the other species of *Erpobdella*. It may be noted that the internal organs of *Erpobdella testacea* are very similar indeed to those of *Trocheta subviridis*, and this fact should be borne in mind when considering relationships within the Erpobdellidae.

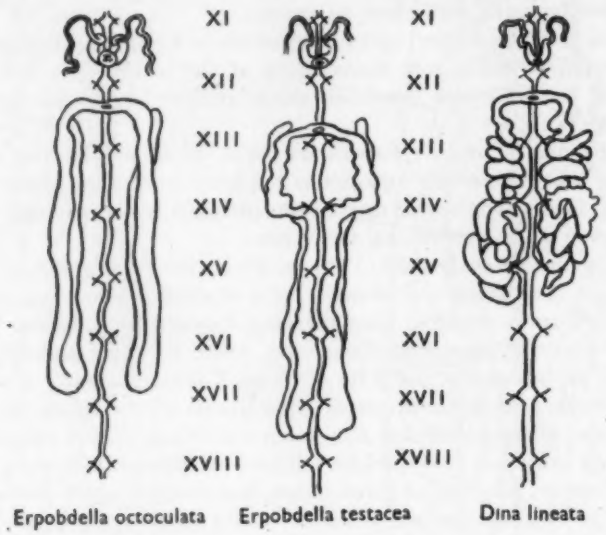

Fig. 3.—Diagram comparing the position and shape of the ovisacs of three species of erpobdellid leech. The male genital atria are indicated anteriorly, and the roman numerals refer to the ganglia of the ventral nerve cord.

HABITAT PREFERENCES OF TROCHETA SPECIES

As has been mentioned previously, Pawlowski (1938 a & b) concluded that the optimum habitat for *T. bykowskii* in the Carpathians is the upper reaches of mountain streams. Perret (1952 a) likewise found that this species lived in the streams of Switzerland and did not enter the lakes. Herter (1937) referred to a communication from Professor Reisinger who collected *Trocheta* from the neighbourhood of Graz, Austria, most of the specimens being taken from the river Mur, but others occurring in small pools among fallen leaves. Reisinger found that leeches from the pools soon died when placed in cages in the river, while the river leeches thrived in the cages, so he deduced that there were two ecological races present. He identified his material as *T. subviridis*, but Pawlowski (private communication) was able to examine some leeches from the river Graz, and found them to be *T. bykowskii*. It is possible that the leeches from the pools were *T. subviridis*. The literature on the latter species suggests that it favours ditches, drains, and sewers in low-lying areas (Harding, 1910 ; Mann, 1955) and that it spends part of the year foraging

in moist soil for earthworms. On the whole, the preference of *T. bykowskii* for well aerated, cool running water, and *T. subviridis* for sluggish, poorly aerated water seems well defined, the chief exceptions being the records by Blanchard (1892) of *T. subviridis* from a clear, cold brook near Genoa, and by Dresschner & Engel (1955) of *T. bykowskii* from swampy situations in Holland and Belgium.

In April 1958 the author studied the distribution of *Trocheta bykowskii* in Windermere and the inflowing streams. A few large specimens were found on the lake shore just north of Troutbeck mouth (National grid reference 394996), this being the site at which they had been discovered by Mr Allanby. The leech was even more abundant in Troutbeck itself, numerous specimens being found in the first quarter of a mile from the mouth of the stream, and smaller numbers over the next quarter of a mile. The leeches appeared to decrease in size as one passed up the river bed, suggesting that only young ones are present in the higher parts, and that the population is spreading upstream.

No other specimens were obtained on the lake shore, but small populations were present at the mouths of three other streams running into Windermere on the east side, viz.: Holbeck (National grid reference 385019, Mill Beck (402977), and a small unnamed stream which enters the lake at Bellman Landing (393938). A number of streams on the west side of Windermere were visited, but no specimens of *T. bykowskii* were discovered. The explanation which best fits the facts of this distribution pattern is that the leech was brought to the shore of the lake near Troutbeck mouth a number of years ago, and from here it has spread up Troutbeck itself and has spread along the lake shore, establishing itself at the mouths of a number of streams on the east side, without becoming established on the lake shore. In all cases, small specimens were found under stones in the water, a few feet from the shore, but larger specimens were found under stones which were resting on damp soil a little way above the water's edge. Examination of gut contents showed that the leeches had been feeding on the oligochaets which are abundant in this situation. There is, however, another species of leech, *Haemopis sanguisuga*, which feeds on the oligochaets in this way and there are many places on the lake shore where this leech is abundant. It seems unlikely that *T. subviridis* would be able to establish itself on those parts of the shore where *Haemopis* is already present, and may explain why *Trocheta* is virtually confined to the streams. The situation is analogous to that found by Pawlowski (1938 b) in the Carpathians, where *Haemopis* occupied the lower reaches of the streams and *Trocheta* the upper reaches. *Haemopis* is less well adapted to life in or near fast flowing water, since its cocoons are deposited loosely under stones, and would be swept downstream in times of spate, whereas the cocoons of *Trocheta* are cemented firmly to stones. It will be interesting to follow the spread of *T. bykowskii* in the Windermere basin, and to look for evidence of competition with *Haemopis*.

HABITAT PREFERENCES OF OTHER ERPOBDELLIDAE

In a previous study of the ecology of leeches (Mann, 1955), adequate data on habitat preferences were obtained for only one species of erpobdellid,

E. octoculata. This leech was found in almost all kinds of water, and was the most abundant species in soft water lakes and ponds, and in streams with stony beds. Concerning the other species it was possible to say little owing to the infrequency of their occurrence. During the past six years the other species of erpobdellids have been collected whenever the opportunity arose, and one can now obtain a clearer picture of their habitat preferences.

Erpobdella testacea appears to thrive in aquatic habitats which are in an advanced stage of colonisation by emergent aquatic plants, particularly *Sparganium* and *Acorus*. It has been found in fifteen such places in the Reading area. The most dense populations are found in ponds where the reeds have grown almost to the centre, and where the water is shallow. In such a situation there is a considerable accumulation of partially decayed organic matter on the bottom, under only a few inches of water, and in summer the oxygen content of the water may be very low indeed. Evidence has been presented elsewhere (Mann, 1956) to show that *E. testacea* may be better fitted for life in a low oxygen concentration than *E. octoculata*. The author knows only one habitat of this type in the Lake District, but it contains many hundreds of *E. testacea*.

Through the generous assistance of Mr T. Warwick of the Department of Zoology, Edinburgh University, many habitats in the Edinburgh area which appear to be suitable for *E. testacea* have been searched but without success. Collections of leeches from other parts of Scotland have also been examined, and it seems that *E. testacea* may well be absent from Scotland.

Dina lineata has been found in only three places in the Reading area, and in only one of these is it at all abundant. This habitat is a small pond which dries out in summer in exceptionally dry years. A single specimen was collected in a ditch on Anglesey in 1955, and forwarded to the author by Dr T. Reynoldson, of University College of North Wales, Bangor. In April 1958 the author visited Anglesey and found specimens of *Dina* in a lake near the Bulkeley memorial, Beaumaris, and in a lake south of Newborough. In each case the leeches were in beds of *Iris* growing in deep soft mud under only an inch or two of water. It was obvious that these habitats would become relatively dry in the event of a drought. Mr T. Warwick has succeeded in finding *Dina* in twelve localities in the Edinburgh area, and most of these were visited by the author in April 1958. The leech was most abundant in two localities, a small pond in woodland at Newliston, which the forester assured us dries out in most summers, and in an area of swamp at Gladsmuir, near Haddington. Several of the other localities were comparable with those described for Anglesey, i.e. *Iris* beds on the fringes of lakes. From these field observations it is clear that the optimum habitat for *Dina lineata* is a small body of water which occasionally dries out, and that it can also establish itself in the *Iris* fringe of a larger body of water, if the water level is liable to fall in dry weather.

It is now possible to put forward a scheme of the distribution of the erpobdellid leeches in Britain. In all permanent and open bodies of water, except certain acid waters in which no leeches occur, *Erpobdella octoculata* is likely to be the most numerous erpobdellid present. As the basin becomes colonised

by emergent aquatic plants such as *Sparganium*, *E. octoculata* tends to be replaced by *E. testacea*. If the situation is such that in a dry season there may be no water standing above the mud (*Iris* often grows in these conditions) then the most numerous erpobdellid is usually *Dina lineata*. *E. testacea* has not been discovered in Scotland, and it is possible that the species has not spread so far north, and that here its place is taken by *Dina lineata*. In running water, *E. octoculata* is usually abundant, but in torrential streams where no other leech can survive being swept away, *Trocheta bykowskii* survives by leaving the water and sheltering under stones in damp places. *Trocheta subviridis* is also amphibious, but appears to travel several hundreds of yards away from the streams where it breeds, apparently in search of earthworms in cultivated soil. It appears to be associated with polluted streams.

SUMMARY

1. *Trocheta bykowskii*, a leech new to Britain, has been found in Windermere (English Lake District) and in Belfast, Northern Ireland. The author considers that it is a valid species.

2. Previous records of this leech are chiefly from the Polish Carpathian mountains, where it occupies the upper reaches of mountain streams. It has also been recorded from Austria, Switzerland and the Netherlands.

3. In Windermere it is apparently in the process of colonizing the inflowing streams on the eastern side of the lake.

4. The taxonomy and the habitat preferences of the other British erpobdellid leeches are also discussed.

ACKNOWLEDGMENTS

I wish to thank Mr C. S. Woods and Mr J. D. Allanby for supplying specimens and information, Dr T. B. Reynoldson and Mr T. Warwick for generous assistance with field observations, and the Director and staff of the Windermere Laboratory of the Freshwater Biological Association for the provision of excellent facilities.

Professor A. Graham kindly read and criticized the manuscript, and the Research Board of the University of Reading provided a travel grant.

APPENDIX

Observations on *Trocheta bykowskii* Gedroyć in Belfast.

By C. S. Woods, B.Sc.*

Trocheta bykowskii has been found in two localities in Belfast, County Antrim. In 1952 a single specimen was taken from a small stream carrying drainage water from the hothouses in the Botanic Gardens Park. Further specimens were collected in December 1956, and on more recent occasions up to twenty individuals have been seen in this stream. The largest specimen measured 16 cms. when moderately extended, and weighed 1·72 gms. when surface water had been removed.

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Early in 1957 specimens of *Trocheta bykowskii* were discovered in a pond close to the River Lagan 2½ miles from the centre of Belfast (Lat. 54° 33·0′N., Long. 5° 56·5′W.). They were all found near the outflow of the pond, in mud under stones, wood, or *Glyceria*, but never in more than a few inches of water. Some have also been found in a bank of damp soil, a few inches above water level.

Both localities are in areas of swamp. The stream receives water from a swampy area in the Botanic Gardens Park. The pond is surrounded by swampy ground and fringed by willows ; a small spring provides the inflowing water and the outflow passes to an area of swamp before running into the River Lagan. It has been noticed that the leeches are not present in the black anaerobic mud, but are in places where there is partially decayed organic matter mixed with fine inorganic silt. Aggregations of several specimens are frequent.

Observations on the associated fauna, and on regurgitated remains of food organisms suggest that when out of water these leeches feed on lumbricid worms and occasional slugs, but that when in the water they take *Tubifex*, and chironomid larvae. It was found that undigested remains of food organisms are often regurgitated twenty-four to sixty hours after they have been swallowed.

It is interesting to note that the other leech which has the same feeding habits, *Haemopis sanguisuga*, has not been found in the Botanic Gardens Park and, although looked for, only a single specimen has been observed at the pond. It was in the bank of damp soil a few inches from two specimens of *Trocheta*. *Haemopis sanguisuga* is common in certain localities in the Belfast area.

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STUDIES ON THE PARASITIC PROTOZOA OF WILD MICE FROM BERKSHIRE WITH A DESCRIPTION OF A NEW SPECIES OF *TRICHOMONAS**

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(With 5 figures in the text)

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INTRODUCTION

The trapping was undertaken during the summers of 1956 and 1957 at the Imperial College Field Station at Silwood Park in Berkshire.

The only previous published work on the parasitic Protozoa of a wild population of small mammals in Britain was that of Elton *et al.* (1931) and that of Jacobs (1952) although Coles (1914) made a survey of the blood parasites of British mammals, birds and fishes. I was fortunate to have access also to some unpublished work by Miss J. Mahon, consisting of a preliminary survey of the Protozoa of rodents of Silwood Park.

The work of Elton *et al.* was primarily an ecological study. The parasitic Protozoa and helminths of a wild population of mice and voles were examined with the aim of determining whether there was any seasonal or age variation and whether these factors could account for the seasonal cycles in the numbers of small rodent populations. No positive results were obtained. There was no sign of a seasonal variation although parasitic populations were found to vary to some extent with the age of the host.

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My original intention was to undertake a survey, similar to that of Elton *et al.*, of the parasitic Protozoa of rodents of the Silwood Park area and to compare the results with those obtained by these authors in the Oxford area. During the course of this work a new species of *Trichomonas* and a species of *Chilomastix*, not previously reported from these hosts, were detected. It was also found that the taxonomy of the flagellate generally known as *Hexamita muris* was in a very confused state and an attempt was made to clarify it.

This part of the work developed to such an extent that it is, in effect, a morphological, rather than ecological study. It is, however, still interesting to compare the incidence of the parasitic Protozoa of the two areas.

MATERIAL AND METHODS

The rodents studied were *Apodemus sylvaticus* (the long-tailed field mouse), *Clethrionymus glareolus* (the bank vole) and *Microtus agrestis hirtus* (the short-tailed vole). They were trapped in " Oxford " traps containing straw for bedding and grain which provided food for the trapped animals.

The animals were examined in the usual way. Smears taken from the gut were fixed exclusively in Schaudinn's fluid with added acetic acid, and stained in Mallory's phosphotungstic haematoxylin or, more often, in Heidenhain's iron haematoxylin. Excellent results were also obtained using Moskowitz's modification of the Bodian technique (Moskowitz, 1950). Blood smears were stained in Giemsa stain.

INCIDENCE OF KNOWN PROTOZOAL PARASITES

Elton *et al.* (1931) surveyed the parasites (Protozoa and helminths) of small rodents in Bagley Wood, Oxfordshire. This was primarily an ecological study. Most of the work was on *Apodemus sylvaticus* but smaller numbers of *Microtus agrestis hirtus* and *Evotomys glareolus* (=*Clethrionymus glareolus*) were also examined.

The figures obtained by Elton *et al.* on incidence of protozoal parasites in mice from Bagley Wood, and my own on incidence at Silwood Park are summarized in Table 1. It is obvious that the numbers of *Microtus* examined from Silwood Park are too small to be significant. However, the numbers of *Clethrionymus* and *Apodemus* are large enough to be of some use for comparative purposes.

The incidence of trypanosomes, Haemosporidia and *Giardia* is approximately the same in the two areas. There is, however, an oustanding difference in the occurrence of *Entamoeba muris* which was found in 50 per cent of *Apodemus* and in 41·4 per cent of *Clethrionymus* in Oxfordshire, whereas at Silwood Park it was found only once in fifty-three *Apodemus* and twice in thirty-one *Clethrionymus*. It is possible that a few infections with *Entamoeba muris* have been missed owing to the enormous numbers of *Trichomonas muris* sometimes present in the caecum, but this factor could hardly account for such a large difference.

It is also interesting that *Trichomonas muris* was found in all of the thirty-one *Clethrionymus* at Silwood Park, whereas Elton *et al.* described it as being of rare occurrence in the same host in the Oxford area. There is a similar

TABLE 1

Incidence of protozoal parasites in mice from Oxford and Berkshire.

Protozoan	Host	Incidence at Oxford Elton *et al.* (1931)		Incidence in Berkshire 1956–7	
		Number examined	Infected percentage	Number examined	Infected percentage
Trichomonas muris	*Apodemus*	443	66	53	75
	Clethrionymus	118	16	31	100
	Microtus	51	96	4	100
Syndyomita (=*Hexamita*) *muris*	*Apodemus*	443	47	53	75
	Clethrionymus	118	12	31	97
	Microtus	51	71	4	75
Eimeria falciformis	*Apodemus*	380	38	53	9·5
	Clethrionymus	84	36	31	3
	Microtus	40	38	4	0
Entamoebc muris	*Apodemus*	443	50	53	2
	Clethrionymus	116	41	31	6·5
	Microtus	51	47	4	25
Trypanosomes	*Apodemus*	580	0·5	52	0
	Clethrionymus	192	11	31	9·5
	Microtus	16	19	2	0
Haemosporidia	*Apodemus*	580	0	52	0
	Clethrionymus	192	0	31	6·5
	Microtus	16	0	2	0
Giardia	*Apodemus*	149	6	53	28
	Clethrionymus	36	94	31	84
	Microtus	10	100	4	100

difference in the distribution of *Syndyomita* (=*Hexamita*) *muris* which was also described by Elton *et al.* as being rare in *Clethrionymus* but was found in 97 per cent of bank voles from Silwood Park. On the other hand Elton *et al.* found *Eimeria falciformis* in thirty out of eighty-four bank voles whereas it was present in only one from Silwood Park, and in that specimen it was extremely rare.

The reason for this difference between my results and those of Elton *et al.* is not clear. This comparison is at least interesting as an indication that the incidence of parasites may vary widely even between two geographically close populations of the same host species, bearing in mind the time lag between the two investigations.

TRICHOMONAS SPECIES IN MICE AND VOLES

Three species of the genus *Trichomonas* were encountered, of which *T. muris* had been previously reported.

TRICHOMONAS MURIS (Grassi, 1879)

The most comprehensive description of *T. muris* was that of Wenrich (1922) who studied it in *Mus musculus* and *Peromyscus*. He gave an account of cell-division which differed in several respects from the previous accounts of Kuczynski (1914, 1918) and Kofoid & Swezy (1915). Elton *et al.* (1931) found *T. muris* in *Apodemus sylvaticus*, *Clethrionymus glareolus* and *Microtus agrestis*.

In the present investigation, *T. muris* was found in forty out of fifty-three *Apodemus*, in all of thirty-one *Clethrionymus* and in all of four *Microtus*. It is interesting to note that the parasite occurred throughout the small intestine and caecum of a large proportion of infected animals. In Wenrich's material, on the other hand, it was apparently confined to the caecum. He found it rarely in the small intestine and then only at the lower end, i.e. close to the caecum.

Very often, the trichomonads from the upper end of the duodenum were much slower-moving than those in the caecum. This may have been a sign that the environment was unfavourable but no signs of degeneration were obvious in fixed and stained preparations from the duodenum.

Division stages of *T. muris* were occasionally encountered during the course of the study but were seen in large numbers in only one specimen of the short-tailed vole. My observations on this process agree in most details with those of Wenrich. There are definitely six chromosomes as described by that author.

Autotomy in T. muris (Fig. 1)

Trichomonad flagellates found in one specimen only of *Apodemus sylvaticus* were at first believed to be undergoing a different division process but this is more probably an example of autotomy.

In the living material it was observed that a large proportion of individuals were much more elongate than is usual for *T. muris* and that the undulating membrane extended only part of the way along the body, which was constricted at the point at which the posterior flagellum became free. Locomotion was rather slow, the course being spiral but complicated by the inactive posterior part of the body which fell slowly from side to side and considerably reduced the momentum.

In fixed preparations from this one specimen, a variety of forms occur which seems to represent stages in a continuous elongation process. Some individuals, such as that shown in Fig. 1a, appear to be normal specimens of *T. muris* except for the presence of a cluster of chromatic granules near the base of the axostyle.

In other individuals (Fig. 1b) there is a slight indication of an elongation and twisting of the posterior part of the body.

The majority of forms are much more elongate, measuring 16·4μ–31μ in length. The width is 3·3–5·8μ although in parts the body may measure as

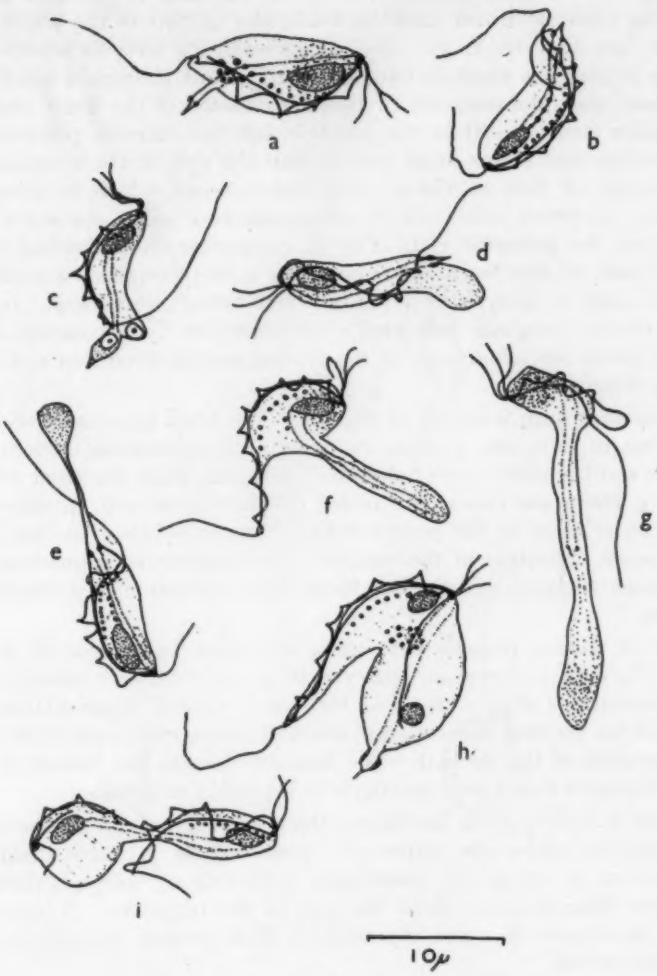

Fig. 1.—Autotomy in *Trichomonas muris*. a–g were drawn from smears stained in Heidenhain's iron haematoxylin. h and i were drawn from smears stained in Mallory's phosphotungstic haematoxylin. a. This shows the aggregation of granules about the base of the axostyle in an otherwise normal specimen of *T. muris*. b–g. These represent various stages in the elongation of the body. h. A binucleate form showing some signs of a mitosis, there being an indication of the remains of a paradesmose. i. A binucleate form apparently consisting of two daughter individuals held together by a common axostyle.

little as 1μ across. In some cases, such as that shown in Fig. 1d, the prolongation of the body occurs to one side of the axostyle and contains no visible organelles. In the great majority, however, the body is extended along the line of the axostyle which runs the whole way or part of the way along the extension (see Fig. 1e, f, g). Fig. 1f represents a form in which the outgrowth is lateral, the axostyle having curved almost through a right-angle.

In these cases the posterior or lateral extension of the body contains no other visible structures than the axostyle but the extreme posterior end is more granular and stains more deeply than the rest of the cytoplasm, with the exception of that at the extreme anterior end which is always more chromatic. However, a few individuals contain two nuclei, one at the anterior and one at the posterior end. Fig. 1i represents an individual with the posterior part of the body also containing a blepharoplast, a rudimentary basal rod and a fairly well-developed undulating membrane. In fact it consists of two daughter individuals held together by a common axostyle. The two nuclei are apparently in the typical resting condition and show no sign of a recent mitosis.

Yet another form is shown in Fig. 1h. The body appears to be in course of splitting in two, one portion containing the undulating membrane, the basal rod and the outer row of chromatic granules while the other retains the axostyle. There are two small nuclei, one in the normal anterior position and the other close to the posterior end of the axostyle. In this specimen there is some indication of the remains of a paradesmose connecting the two nuclei which suggests mitosis, but there is no indication of a duplication of organelles.

It is, of course, possible that these are merely abnormal or degenerate forms. They were, however, observed in an active living condition and in fixed preparations showed none of the usual signs of degeneration such as absence of the flagella, separation of the undulating membrane from the body or enlargement of the nucleus. The binucleate forms are difficult to explain but the elongate forms may be stages in a process of autotomy.

Kofoid & Swezy (1915) mentioned the occurrence of this process in *Trichomonas augusta* under the name of "plasmecdysis". They described the accumulation of cytoplasm posteriorly producing a "sub-spheroidal blob" which was then detached from the rest of the organism. It contained no nuclear structures or other chromidia. This process apparently bore no relation to mitosis.

Wenrich (1944), however, observed autotomy in *T. vaginalis* of man and suggested that the process might serve as a stimulus to division, as he found more division stages among smaller than among larger parasites. Trussell (1947) confirmed the repeated occurrence of autotomy in *T. vaginalis* in culture and concluded that it was apparently a normal phenomenon.

TRICHOMONAS MICROTI Wenrich & Saxe, 1950 (Fig. 2)

A species of *Trichomonas* present in the caecum of a single specimen of *Apodemus* was found to be distinct from *T. muris* and closely resembled

T. microti Wenrich & Saxe, 1950 which was originally described from *Microtus pennsylvanicus*.

T. microti is smaller than *T. muris*, measuring 5·4–7·4μ in length and 2·7–4·1μ in width. The body is approximately ovoid, the anterior end being slightly more rounded than the posterior.

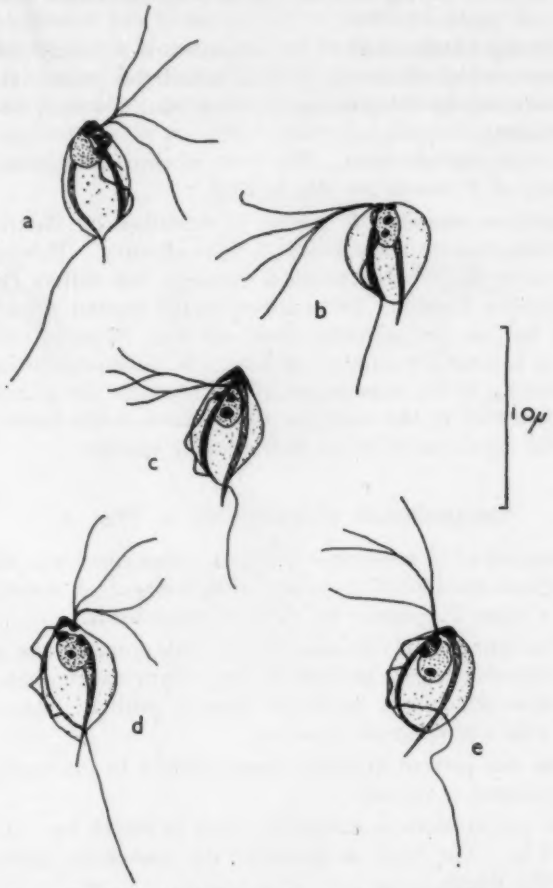

Fig. 2.—*Trichomonas microti* Wenrich & Saxe. Drawn from smears impregnated with protein silver.

The nucleus is anterior and contains an eccentric endosome which is not surrounded by a clear area as it is in *T. muris*.

There are four anterior flagella as long as, or slightly longer than, the body and arising from a single blepharoplast anterior to the nucleus. Also arising from the blepharoplast are a deeply-staining chromatic basal rod and an undulating membrane with three or four undulations. The free part of the posterior flagellum is about as long as the anterior flagella.

The axostyle is less hyaline than that of *T. muris* and in fact stains quite darkly in silver. It projects from the body for about 1 to 1½μ but has no chromatic ring at the point of emergence.

Overlying the front of the nucleus are three granules which, according to Wenrich & Saxe, represent the parabasal body. These authors also described a Y-shaped strand overlying the nucleus in some specimens but this was not observed.

At the extreme anterior end of the organism is a darkly-staining, wedge-shaped structure which Wenrich & Saxe called the pelta. It forms a cap and tends to obscure the blepharoplast which can, however, be distinguished by careful focussing.

No cystostome was observed. The rows of chromatic granules which are so characteristic of *T. muris* are also lacking.

These flagellates resemble *T. microti* as described by Wenrich & Saxe so closely that there can be little doubt of their identity. This species bears a close resemblance to *Pentatrichomonas hominis* but differs from it in the number of anterior flagella. The number in the human species varies from three to five but in the majority there are five (Wenrich, 1944), whereas *T. microti* has a constant number of four. It is clearly distinguished from *T. muris*, differing in the appearance of the nucleus, the number of anterior flagella, the structure of the axostyle, the absence of chromatic granules and the form of the parabasal body, as well as being smaller.

TRICHOMONAS SYLVATICI sp. n. (Fig. 3)

A small species of *Trichomonas* hitherto undescribed was detected in the caecum of several specimens of *Apodemus sylvaticus*. A description is given below and the name *T. sylvatici* sp. n. is proposed for it.

This species cannot easily be observed in fresh preparations, partly because of its small size and partly because of the enormous numbers of the much larger *T. muris* which are normally present with it. Another confusing factor is the wide size range of *T. muris*.

T. sylvatici was present in fairly large numbers in the caeca of six out of seventeen *Apodemus* examined.

In stained preparations it measures 3–10μ in length by 1–3μ, the average being $7{\cdot}9\mu \times 2{\cdot}7\mu$. The body is fusiform, the maximum width being about one-third of the length.

The nucleus is oval, measures on the average 2μ in length and lies in the anterior half of the body beside the axostyle. An eccentric endosome is present but this is not usually surrounded by a clear area as it is in *T. muris*.

The blepharoplast is large and lies at the extreme anterior end of the body. In some silver preparations it appears to consist of three lobes which suggests that it may be a compound structure. In preparations stained in Heidenhain's haematoxylin the blepharoplast is very lightly stained but in Mallory's phosphotungstic haematoxylin and in protein silver it stains very deeply.

The posterior flagellum, forming the edge of the undulating membrane, does not stain deeply as does that of *T. muris*; in fact the edge of the membrane appears to be no thicker than the free part of the flagellum.

The course of the undulating membrane is not as clearly a spiral as it is in *T. muris*. It runs down one side of the body (on the same side as the nucleus) and then crosses behind the axostyle at the level of the chromatic ring. The undulating membrane has three to five undulations along its course. The free part of the flagellum is one-and-a-half to twice the length of the body.

The exact number of flagella is difficult to determine. In silver preparations most individuals show three quite clearly but some of those stained in Mallory's appear to have four. This is rather uncertain, however, and it seems that

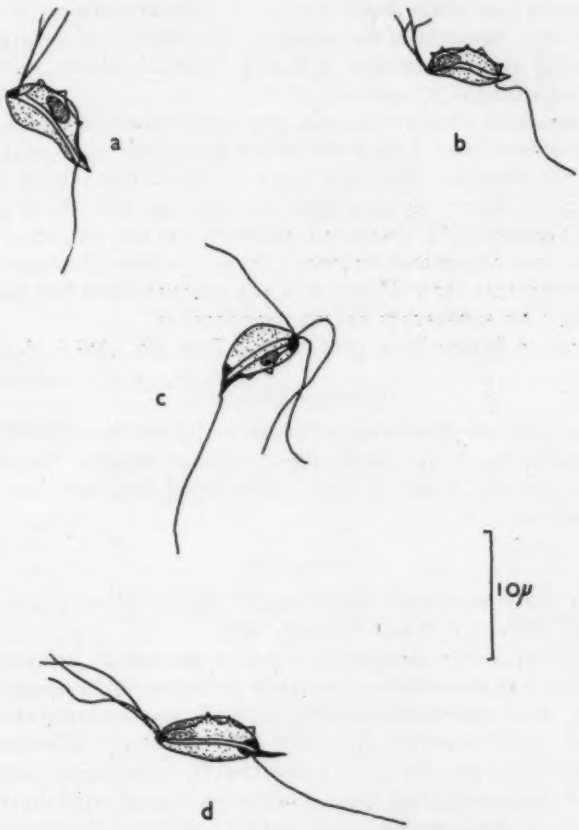

Fig. 3.—*Trichomonas sylvatici* sp.—n. a. A specimen stained in Mallory's phosphotungstic haematoxylin. b. This was stained in Mallory's and appears to show four flagella. c and d. Specimens stained in protein silver showing three clear anterior flagella. The chromatic ring and the chromatic tip of the axostyle are also shown.

most individuals have three anterior flagella only. They are equal in length and about the same length as the body, i.e. relatively much longer than those of *T. muris*.

The axostyle is hyaline and slightly curved. It projects posteriorly for a variable distance, usually about 1–2μ. At the point of emergence from the body there is a very pronounced chromatic ring which is particularly well shown in silver preparations in which the projecting tip of the axostyle is also chromatic.

A particularly striking difference from *T. muris* is the absence of a chromatic basal rod beneath the undulating membrane. The inner and outer rows of chromatic granules, characteristic of *T. muris*, are also lacking, although there are occasionally a few small scattered granules in the region of the nucleus.

This species is also quite distinct from *T. microti*, differing in the general shape of the body, the form of the axostyle, the absence of a chromatic basal rod and probably also the number of flagella, which is almost certainly three as compared with four in *T. microti*.

No structures were observed in this species which could represent either a cytostome or a parabasal body. It is interesting to note that the silver impregnated preparations, although fixed in Schaudinn's fluid with acetic acid, showed quite clearly the parabasal body in some individuals of *T. muris*. According to Wenrich (1922) acetic acid dissolves out the parabasal apparatus.

T. sylvatici does not appear to form " cysts " as does *T. muris*. Preparations of rectal contents show *T. muris* in the rounded state but this species is represented only by apparently normal trophozoites.

Type: Deposited British Mus. (Nat. Hist.). Reg. No. 1958.8.26.1.

Differential diagnosis

A small species of *Trichomonas* parasitic in the caecum of *Apodemus sylvaticus* ; measuring 3–10μ ; with three anterior flagella, the same length as the body, arising from a large, three-lobed blepharoplast ; lacking a chromatic basal rod.

Discussion

Until 1924 the trichomonad flagellates of mice were considered to belong to one species, namely *T. muris* (Grassi, 1879).

Wenrich (1924) briefly described a smaller species, *T. minuta*, from rats and mice. This was described as similar in structure to *T. muris* but smaller and with only three chromosomes in division (*T. muris* having six).

Elton *et al.* (1931) reported *T. muris* from *Apodemus sylvaticus*, *Microtus agrestis* and *Evotomys glareolus*, and noted that in young mice which had been newly infected the parasite was much smaller because of rapid division. There was no mention of these smaller forms having a different structure.

Morénas (1938) found a small species in *Mus musculus* which he believed to be *T. minuta*. He described it as measuring 5–7μ in length (i.e. smaller than *T. muris*) with an abnormally large blepharoplast and apparently lacking a chromatic basal rod.

TABLE 2

Comparison of the three species of *Trichomonas*

	T. muris	*T. microti*	*T. sylvatici*
Hosts	*Apodemus* *Clethrionymus* *Microtus*	*Apodemus*	*Apodemus*
Situation	caecum small intestine	caecum	caecum
Body shape	pyriform or fusiform	ovoid	fusiform
Length	6–20μ	5·4–7·4μ	3–10μ
Nucleus	central or eccentric endosome surrounded by clear area	eccentric endosome no clear area	eccentric endosome no clear area
Blepharoplast	Possibly double	small, single	relatively large ; three lobes ?
Anterior flagella	3—one-third to one-half body length	4—same length as body or longer	3 (possibly 4) same length as body
Undulating membrane	6–8 undulations	3–4 undulations	3–5 undulations
Free part of posterior flagellum	same length as body	same length as body	1½ to 2 × body length
Costa	very chromatic	chromatic	absent
Chromatic granules	2 rows	absent	absent
Axostyle	Hyaline, chromatic ring present	stains deeply, no chromatic ring	hyaline, chromatic ring present
Parabasal body	curved rod over nucleus	3 granules over nucleus. (Y-shaped strand of Wenrich)	none observed
Cystostome	anterior clear area	none observed	none observed
Pelta	Absent	wedge-shaped cap anterior end	absent

Wenrich & Saxe (1950) described *T. microti*, a new species from *Microtus pennsylvanicus*. The authors stated in the discussion of this paper that the species described by Morénas in 1938 was not *T. minuta* as it lacked the characteristic costa (chromatic basal rod) and chromatic granules.

T. sylvatici sp. n., described above, appears to correspond to the species found by Morénas in *Mus musculus* which he mistakenly identified as *T. minuta* Wenrich.

The three species of *Trichomonas* from mice are compared in Table 2.

CHILOMASTIX SP.? IN MICE AND VOLES (Fig.4)

A species of *Chilomastix* was found in the caecum of mice and voles which differs mainly in size from species previously reported from rodents and may be a new species. Specimens were found in four out of fifty *Apodemus*, two out of thirty-one *Clethrionymus* and in two of the four *Microtus*. Infection was usually heavy. The genus has not previously been reported from these hosts.

Morphology

The active flagellate is readily distinguished from *Trichomonas* as locomotion is much slower and consists of a slow rotation about the longitudinal axis. The body is elongate with a rounded anterior end. The posterior end may taper gradually to a point or it may be rounded and finish abruptly in a sharply pointed " tail ". The nucleus is sometimes visible as a clear ring at the extreme anterior end. Three long anterior flagella can also be made out but the buccal flagellum is very difficult to see. The posterior half of the body is flattened slightly and there is some indication of a spiral twist, the exact nature of which is not quite clear.

In fixed and stained preparations the body is pyriform, the anterior end being rounded, the posterior end tapering gradually to a sharp point.

The length ranges from 6·6 to 16·5μ. There is some difference in size between the forms in *Apodemus* and those in *Clethrionymus*. The average in the former is 12·6μ and in the latter 9·3μ. However, they appear to be identical in structure.

The width of the cell ranges from 5 to 8μ with an average of 6·5μ for all three host species. Thus the ratio of length to width is greater in specimens from *Apodemus* than it is in those from *Clethrionymus*, some of the latter having an almost spherical appearance.

The cytostome is anterior and lateral and measures approximately 5μ in depth and 2μ in width. A single peristomal fibre runs along the outer margin of the cytostome and curls round at the base. It stains very deeply. In *C. mesnili* of man there is a second peristomal fibre on the inner margin of the cytostome which was not observed in this species.

The nucleus lies in an anterior position beside the cytostome. It is spherical and averages 2·5μ in diameter. Lying on the nuclear membrane are several lenticular masses of chromatin which gives the nucleus the appearance so characteristic of the genus *Chilomastix*. Most often there are two of these masses lying one at the anterior and one at the posterior pole of the

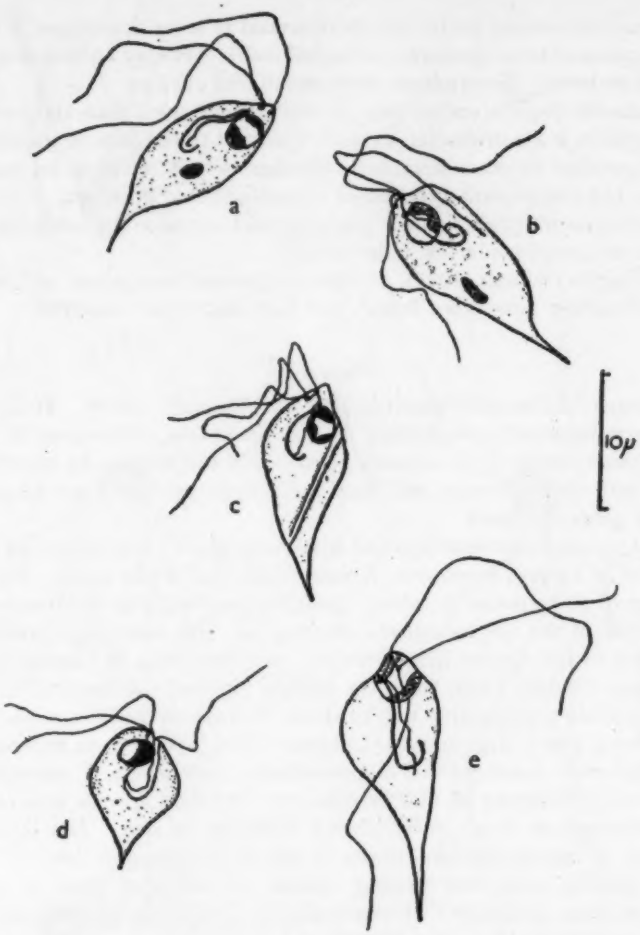

Fig. 4.—*Chilomastix* sp. from mice and voles. Drawn from smears impregnated with protein silver. d. A specimen from the caecum of *Clethrionymus glareolus*. The remaining figures represent specimens from the caecum of *Apodemus sylvaticus*.

nucleus and separated from each other by nuclear membrane devoid of chromatin. There is no endosome.

Anterior to the nucleus are three blepharoplasts giving origin to the flagella and the peristomal fibre. The arrangement of these structures is not easy to make out in haematoxylin preparations but silver preparations were found to be quite satisfactory. Two of the three blepharoplasts lie side-by-side at the anterior end connected by a rhizoplast. One blepharoplast (b1) gives rise to two flagella and the other (b2) to a single flagellum. Posterior to these and lying against the nucleus is the third granule (b3) which gives origin to the peristomal fibre and to the buccal flagellum which lies in the cytostome.

A rhizoplast connecting b3 to b2 was observed in some specimens, whereas in others it appeared to be similarly connected to b1. It may be that it is actually connected to both. No separate centrosome was obvious.

The anterior flagella are as long as or slightly longer than the body. The buccal flagellum is much shorter, extending almost to the base of the cytostome. It is not possible to state definitely whether or not it forms an undulating membrane but the general appearance suggests that it does not.

The cytoplasm appears finely granular and occasionally alveolar. Large inclusions are present in a few individuals.

According to Geiman (1935), division stages are always rare in *Chilomastix* and unfortunately none were found, nor were any cysts observed.

Discussion

The genus *Chilomastix* was founded by Alexeieff (1910). It appears to have a very constant morphology except for minor differences in size and shape. Consequently it is not easy to separate the species on morphological grounds, and although size and host-preference are not good criteria they have been generally used.

Several species have been reported from rodents. *C. bettencourti* da Fonseca, 1915 occurs in *Epimys norvegicus*, *Epimys rattus* and white mice. The original description of this species is rather confusing, particularly with respect to the arrangements of the blepharoplasts and flagella. Its size-range does however overlap that of the species described here and they may be identical.

C. magna Becker, 1926, from the ground squirrel *Citellus tridecemlineatus* is larger and has a distinctive tuft of short cuticular structures at the anterior end. There is also a large species *C. oblonga* Chang, 1935, from another ground squirrel *Eutamias asiaticus* and a species from guinea pigs, *C. intestinalis*.

C. mesnili (Wenyon) of man is the best-described species and closely resembles this species from mice, though differing in size. The latter varies much more in length and the minimum size is considerably less.

It is possible that two distinct species are included here, a larger one parasitic in mice (probably *C. bettencourti*) and a smaller one in voles. However, this could only be proved by culture methods which would provide more division stages or by attempting artificial infections. Time did not permit the use of such methods in this investigation.

SYNDYOMITA MURIS (=*HEXAMITA MURIS*) (Fig. 5)

It will be shown below that the valid name for the organisms parasitic in the small intestine and caecum of mice and rats, and generally known as *Hexamita muris*, is probably *Syndyomita muris* n. comb. This flagellate was studied in *Apodemus sylvaticus*, *Clethrionymus glareolus* and *Microtus agrestis hirtus*.

When the literature was consulted in an attempt to determine the exact nomenclatural status of these organisms, such confusion was encountered that it was found necessary to review completely all previous work on *Hexamita* and other related genera. A historical survey of the literature is set out below.

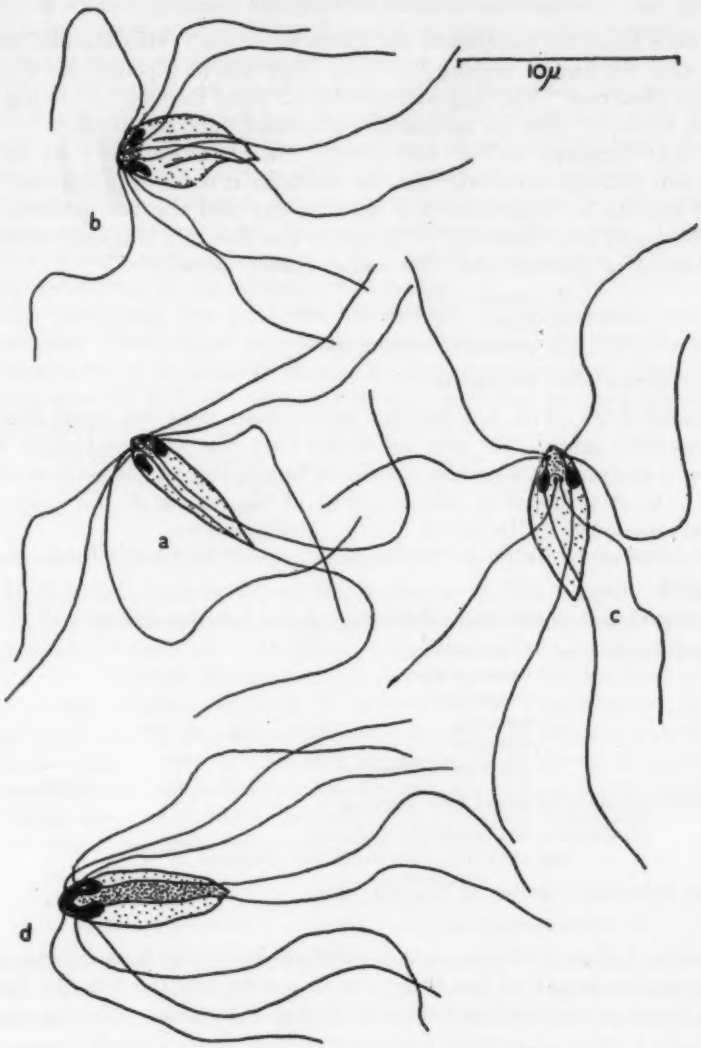

Fig. 5.—*Syndyomita muris* n. comb. a. A specimen from the small intestine of *Clethrionymus glareolus*, stained in Heidenhain's iron haematoxylin. This corresponds with *Hexamita muris* Type A of Wenyon and *Hexamita muris* of Morénas. b. A specimen from the same preparation as (a). This type resembles Grassi's description of *Dicercomonas muris*. c. Also from the same preparation, this specimen resembles von Prowazek's description of *Octomitus intestinalis*. d. A specimen from the caecum of *Apodemus sylvaticus*, also stained in Heidenhain's iron haematoxylin. This represents *Hexamita muris* Type B of Wenyon and *Syndyomita intestinalis* of Morénas.

Survey of the literature

In 1838 Dujardin established the genus *Hexamita*. He described an infusorian with six flagella leaving the body from different points—two anterior and four posterior. His diagram showed six clear flagella. It is important to note, however, that his microscope magnified only 500 times.

In 1841 Dujardin defined the genus. He described the body as being oblong and rounded anteriorly, narrow and bifid or notched posteriorly. Two or four flagella left separately the anterior end and the two posterior lobes were prolonged into filaments. The genus was found in stagnant water or in the intestine of Batrachians. He named three species :—

H. nodulosa, *H. inflata* } from foul water
H. intestinalis from frogs

No type species was designated.

Bütschli (1878), with no apparent justification, used the name *Hexamitus* for Dujardin's genus. He was convinced that this possessed eight flagella and gave a diagram showing this number of flagella leaving the body at different points. He also figured a single nucleus in the middle of the body, which was not mentioned by Dujardin.

Nevertheless, in his book " Protozoen " (1883) he figured *Hexamitus* with six flagella.

In 1882 Grassi classified the following genera into one family :—

Family Cercomonas—*Monocercomonas*
Cimaenomonas
Plagiomonas
Monomita
Heteromita
Dicercomonas (Grassi)

The latter genus contained two species:—

(i) *Dicercomonas intestinalis* (Dujardin)
Synonym—*Hexamita intestinalis*, Dujardin

with an indefinite number of flagella, and

(ii) *Dicercomonas muris* sp. n.

This species had an oval-elongated or pyriform body with four anterior flagella. The maximum length of the body was 6·4μ–4·6μ and the breadth was 2·2μ. It was found in the small intestine of *Mus* and *Arvicola*. No diagrams were given.

In 1888 Grassi defined his genus *Dicercomonas* with four anterior and two posterior flagella.

In 1894 Klebs studied Dujardin's species but he adopted Bütschli's name (i.e. *Hexamitus*). He found eight flagella, two separate bundles at the anterior end, each of three flagella, and two posterior flagella. This author pointed out that the name should, therefore, really be *Octomitus* but he considered it more appropriate to keep the old, established name. He described a single nucleus in the front half of the body. No mention was made of the form from mice.

In 1901 Doflein defined *Hexamitus* with four anterior and two posterior flagella and a single nucleus. He included in this *H. muris* (Grassi), listing *Dicercomonas muris* as a synonym.

In 1904 Prowazek described a new species *Oktomitus intestinalis* from the gut of rats. This species had eight flagella, of which four were directed forwards. All flagella arose from small, round, clearly-defined basal granules. The two caudal flagella originated at the posterior end between the closely applied axial rods. Prowazek did not, however, state that he was founding a new genus and made no formal definition of the genus *Octomitus*. (The name *Oktomitus* is etymologically incorrect and has been rewritten in the correct form, i.e. *Octomitus*, by all subsequent authors).

In the same year Foa published an account of *Dicercomonas muris* and *D. intestinalis*. This author considered it impossible to distinguish the number or arrangements of the anterior flagella in living preparations. Her diagram shows six anterior and two posterior flagella and two anterior nuclei. She divided *Hexamitus* Dujardin into three genera :—

(i) *Hexamitus* Dujardin	free-living
(ii) *Dicercomonas* Grassi	parasitic
D. muris Grassi	
D. intestinalis (Duj.)	
(iii) *Urophagus* Klebs	free-living with posterior cytostomes.

In 1909 Dobell, in a review of the literature on this subject, stated that Foa's solution could not be regarded as a correct one. The name *Dicercomonas* was not available as it has been founded by Diesing for a uniflagellate. He suggested that the name *Hexamitus* Duj. should be retained for the free-living forms with six flagella. He took *H. inflatus* as the type species. For the parasitic forms he took the name *Octomitus* "as originally suggested by Klebs". However, as this was used by Prowazek for a parasite of the rat *O. intestinalis*, a new specific name had to be found for the parasite of frogs previously known as *Hexamitus intestinalis* and he renamed this *Octomitus dujardini*.

Dobell's genus therefore contained three species :—

O. dujardini	from frogs and toads
O. muris Grassi	from rats and mice
O. intestinalis Prowazek	in rats

In 1926 Wenyon, in his textbook "Protozoology", gave an account of *Hexamita muris* (Grassi). He believed that the small, narrow form in the small intestine of mice and the larger, broader form in the caecum belonged to the same species. The smaller form measured 4–7$\mu \times$ 2–3μ, the larger 10$\mu \times$ 5–6μ. He considered the possibility that the larger form might be adults and the smaller ones young.

In 1936 Lavier arrived at the following conclusions—that the generic name must be *Hexamita* Dujardin, 1838 and the type species *H. nodulosa* Dujardin, 1941, and that *Hexamitus* was obviously incorrect. His reasons for disregarding Dobell's earlier selection of *H. inflatus* as the type species are not clear. He considered that Prowazek, when he named *Octomitus intestinalis*, was not intending to form a new genus but was simply using what he considered to be a more correct etymological equivalent. This seems to

be rather doubtful reasoning for, if this were the case, the specific name would clash with that of the parasitic form named by Dujardin in frogs, i.e. *Hexamita intestinalis*. According to this author, Dobell's solution was also incorrect, as the placing of parasitic and free-living forms in separate genera was not based on morphological differences and was therefore invalid. He gave a new description of the free-living forms and *H. intestinalis* and also founded a new genus *Syndyomita* with a species *S. neglecta* from *Salamandra*. Of this species he wrote: "It is a flagellate of this type which was described by Prowazek under the name of *Octomitus intestinalis*, but I believe it expedient, in order to avoid new confusion, not to retain this generic name which Prowazek never defined and which his successors have applied without discrimination to all parasitic *Hexamita*".

In 1938 Morénas studied the intestinal Protozoa of several rodents. He confirmed the existence of two types of *Hexamita* in mice and rats. His type A, the form from the small intestine, he proposed to call *Hexamita muris* (Grassi, 1881). Type B (the "larger, broader form" of Wenyon) which he found only in the caecum of rats, he called *Syndyomita intestinalis* (Prowazek, 1904). It should be noted, however, that Morénas' diagrams of both these forms differ in several respects from Prowazek's diagrams of *Octomitus intestinalis*, particularly in the arrangement of nuclei and blepharoplasts.

Grassé in his "Traité de Zoologie" (1952) retains both *Hexamita* and *Octomitus* as valid genera, separating them on grounds of differences in symmetry. According to this work an individual *Hexamita* appears to consist of two "Zooids" lying side-by-side in such a way that their longitudinal axes cross in an X and that their two sets of organelles are exactly symmetrical with respect to the main longitudinal axis of the body. The roots of the posterior flagella are external relative to the nuclei. This symmetry is easily recognizable from the positions of the "cytostomes" and the intracytoplasmic segments of the flagella. In *Octomitus*, however, the two groups of organelles are symmetrical about a sagittal plane and constitute respectively the right and left sides of the organism.

Grassé has apparently based these conclusions on Lavier's description of *Syndyomita* and not on Prowazek's original description of *Octomitus* which differs from it in several respects. He does, however, name *Octomitus intestinalis* Prowazek as the type species.

Discussion

The taxonomy of these flagellates has become extremely complicated. The basic problem involved in clarification of this issue concerns the status of a genus defined by an incorrect description. The only features mentioned by Dujardin as being characteristic of his genus *Hexamita* were the pyriform shape and the possession of two or four anterior flagella and of two filiform extensions at the posterior end. His diagrams showed no more detail. The next description of free-living forms was that of Klebs who found eight flagella, as have most authors who have described them since. Considering that Dujardin was using a microscope that magnified only 500 times it is almost certain that he made a mistake in the number of flagella. Klebs, however, saw only one

nucleus. It is a purely arbitrary decision as to whether this was another error due to a poor microscope or whether a uninucleate form does exist. All the evidence, however, points to an error. No-one who has studied free-living or parasitic forms since has mentioned uninucleate forms.

The choice therefore lies between three possibilities :—

(a) to regard *Hexamita* Dujardin as a *nomen nudum* and to give the genus a new name and definition;

(b) to accept the genus as defined by Dujardin, i.e. 6-flagellate organisms and to find a new name for the 8-flagellate forms; or

(c) to accept the name *Hexamita* Dujardin as the correct one for these 8-flagellate, free-living or parasitic organisms and to redefine the genus. The last mentioned would seem to be the most desirable since it does not necessitate the introduction of new names which might in their turn add to the complications.

The first really adequate description of free-living forms was that of Lavier, which should therefore be used as a basis for redefining the genus *Hexamita*. A definition based on his description would then read as follows :—

Free-living or parasitic in batrachians. Symmetrical about the longitudinal axis. Two nuclei at the anterior pole, spherical or oval, with axes directed towards this pole. Three blepharoplasts on each side of the anterior pole give rise to three anterior flagella, a fourth lower down gives rise to a posterior flagellum on each side. The posterior flagella run just beneath the surface of the body and before reaching the posterior pole they emerge in small depressions, the cytostomes.

This definition clears the way for the separation of the genus from those forms which are symmetrical about a sagittal plane and in which the axostyles take origin inside the nuclei and run down the body side-by-side. These forms also differ in the absence of cytostomes. The valid name for this genus must be either *Octomitus* Prowazek, 1904 or *Syndyomita* Lavier, 1936. Had Prowazek made it clear that he intended to create a new genus, then his description of *O. intestinalis* would have constituted a definition of that genus, as it was monotypic. However, in actual fact, the genus was never created and has not been formally defined. It cannot therefore exist.

It seems then that *Octomitus* Prowazek should be rejected as a *nomen nudum* and *Syndyomita* Lavier be accepted as the correct name for the genus, *S. neglecta* Lavier being the type species. This genus would also include *S. intestinalis* (Prowazek), and various other parasites of the Amphibia and rodents.

In this investigation a study was made of the flagellate which occurs in the small intestine and caecum of mice and voles, usually known as *Hexamita muris*, but probably correctly named *Syndyomita muris*. The first point to emerge from such a study is the extreme variability of form. Individuals drawn from a single specimen of *Clethrionymus glareolus* are shown in Fig. 5. The caecal form appears to differ considerably in staining properties from the others but they are all in the same size range and it seems more desirable from the point of view of nomenclature to consider all these forms from mice as belonging to the same species. As the relationship to Prowazek's species

from rats is rather obscure (he did not find any great variation in form) the valid name for the species in mice and voles would seem to be *Syndyomita muris* (Grassi, 1882) n. comb.

Synonyms :—(1) *Dicercomonas muris* Grassi, 1882.
(2) *Hexamitus muris* (Grassi, 1882), Doflein, 1901.
(3) *Hexamita muris* (Grassi, 1882) Wenyon, 1926.
(4) *Octomitus intestinalis* Prowazek, 1904.
(5) *Syndyomita intestinalis* (Prowazek, 1904), Morénas, 1938.

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SUMMARY

1. The work consists of a study of the protozoal parasites of wild rodents of the Silwood Park area, Berkshire.

2. A comparison of the figures for the incidence of parasitic Protozoa in *Apodemus sylvaticus* and *Clethrionymus glareolus* at Silwood Park with those of Elton *et al.* for the same hosts in the Oxford area, shows that the incidence of parasites may vary widely between two geographically close populations.

3. Observations of mitosis in *Trichomonas muris* confirm Wenrich's description of the process in that species.

4. Individuals of *T. muris* apparently undergoing autotomy are described.

5. *Trichomonas microti* Wenrich & Saxe, a four-flagellate species, is reported for the first time from *Apodemus sylvaticus*.

6. *Trichomonas sylvatici* sp. n. is described from the caecum of *Apodemus*. This differs from *T. muris* in the small size ($3–10\mu \times 1–3\mu$), in the absence of a chromatic basal rod and chromatic granules and in the possession of a relatively large 3-lobed blepharoplast.

7. A species of *Chilomastix* is reported from the caecum of mice and voles.

8. The literature concerning the taxonomy of "*Hexamita muris*" is surveyed. It is concluded that the forms in mice belong to a single species and that the valid name should be *Syndyomita muris* n. comb. A list of synonyms is given.

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A REVISION OF THE BRITISH SYMPHYLA

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(With 13 figures in the text)

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Order Symphyla Ryder

1880 Symphyla Ryder, Amer. Nat. 14: 375–376.

Head separate, setose, with entognathous mouthparts, two-segmented mandibles with single cranial articulation, maxillae of two segments and second maxillae fused to form a labium. Internal thickening of dorsal integument known as central rod present ; one pair of spiracles only, opening at sides of head. *Antennae* five to sixty segmented with intrinsic muscles in each segment ; setae and sensory organs present on most segments. Eyes absent. Post-antennal organs at base of antennae. *Trunk* of fourteen segments with fifteen to twenty-two scuta, first scutum often reduced or absent. Paired gonads opening without external genitalia, on fourth trunk segment just anterior to fourth pair of legs. Paired sensory organs known as calicles at sides of last scutum, each bearing a very long sensory seta. Twelve pairs of legs, the first usually reduced more or less strongly, sometimes scarcely distinguishable from others. Normal leg consisting of six segments : coxa, trochanter, femur, tibia, tarsus and paired claws ; styli present at bases of last ten pairs of legs, sometimes very reduced ; eversible coxal sacs present between legs 3–9, 3–10, or 3–11, on remaining legs they are degenerate, except on the first where they are absent. Cerci, which are part of thirteenth segment, conical and terminating in one or two longer setae ; with paired silk glands opening near tip.

INTRODUCTION

Only about fifty papers have been written on the taxonomy of the Symphyla and several genera are still in a chaotic state. This is largely due to the amount of variation of characters found in most of the genera studied. Authors have established new species on single damaged specimens, have used characters which are often only local variations, and have often based their descriptions on immature specimens.

In his " Synopsis of the British Symphyla " (1913), Bagnall gives keys and descriptions of thirteen species. Of these only seven can now be accepted for reasons given in this paper. In the present work these seven species are more fully described and a further seven species are described ; including five species new to the British Isles and two species new to science. Wherever possible large numbers of specimens of these species have been collected and the range of variation of the various characters observed and recorded. A statistical treatment of some of the characters, such as numbers of setae on various organs would have been of value, but it has not been found practicable to attempt this here.

OCCURRENCE OF THE SYMPHYLA

Much of the material examined, was obtained in the course of a series of ecological studies of the Order carried out in the South West of England. At first only those species which were of economic importance were collected, but later the survey was extended to include all species.

Symphylids are most abundant in light soils rich in humus, with plants growing at the surface. They are, however, found in a variety of other situations such as in moss, under bark, under stones, among leaf humus, and even in uncultivated barren soils (Michelbacher, 1948).

Wherever specimens were found they were usually present in very large numbers and could be collected readily. Populations of some species as high as 80,000,000 per acre have been estimated in some localities (Edwards, 1955 a). Collection from soil can be easily carried out by breaking open clods of earth so that the runways are exposed. This method, however, is very tedious, and, in addition, at certain seasons many species of Symphyla go down too deep to be found. Hence, where as many specimens as possible are required, the best method of obtaining them is by placing a section of soil in a container of water (Michelbacher, 1939). The symphylids readily float to the surface when the water is stirred, and can be picked up with a fine brush, and if desired kept alive on a plaster of Paris culture medium (Edwards, 1955 b). Alternatively, a Berlese funnel can be used, but the number of specimens recovered from a soil sample are less by this method than by a flotation method.

Specimens are found under a variety of soil conditions, and are often abundant at soil temperatures as low as 2°C and as high as 28°C. They seem to prefer soil with a high organic content and are never found in dry soils, since they require a minimum soil moisture content of about 6 per cent for survival in an average loam soil.

Symphylids have been found at all altitudes. They are frequently found on the banks of rivers and even near the high tide level*. They are common in all types of soils but occur less frequently in clay soils, probably due to the difficulty of constructing runways in clay.

Species of the genus *Scutigerella* were usually found in the soil around the roots of growing plants (an exception is *Scutigerella causeyae* Michelbacher, which is more often found among forest litter, humus, etc.). All British species of the genus with the exception of the latter, have been found to be of considerable economic importance, both under glass and outdoors, since they will attack practically any plant possessing young succulent roots.

Specimens of the genus *Hanseniella* were also found around growing roots in tropical hothouses. Although their food was not determined they were most numerous close to the plant roots.

Specimens of the genera *Symphyella*, *Symphylellopsis* and *Scolopendrella* were more frequently found widely distributed throughout the soil. They were also found around growing roots, but it is believed that they were only feeding on decaying root tissues.

MOUNTING TECHNIQUE

It is important that a standardised mounting technique should be adopted, since a number of characters used in determinations are comparative. In the present study three main methods have been used. All specimens have been stored in 70 per cent alcohol to which a little glycerine has been added. For determinations specimens have been examined as temporary mounts in lactic acid under a cover slip, and gently warmed for about 10 min. to clear them.

Two types of permanent mount have been used. A number of specimens from each locality were mounted in polyvinyl alcohol Type A3 (Salmon,

* I have been informed by Dr H. E. Hinton that he has seen a species below high tide level at Yealmpton, Devon.

1951). This is made up by first heating 60 gm. Phenol Detached Crystals B.P. with 60 c.c. lactic acid B.P. Then to 15 c.c. Elvanol 51 A 05 polyvinyl alcohol, 15 c.c. distilled water is added drop by drop. This gives a fluffy paste which may be cleared by gently heating on a water bath. When specimens are mounted in this medium they should be left to set in an oven at about 50°C. This extends the appendages very satisfactorily. Such mounts have been kept four years with very little deterioration. A further refinement is to add a few grains of the stain lignin pink to the medium. This is taken up by the specimen and makes observations of setae and other structures very much simpler. Most of the drawings were made from this type of mount, since P.V.A. has the advantage of extending the specimen, a feature of great value in examining specimens with large numbers of legs.

The alternative type of permanent mount was made in the following way : the specimen was cleared for forty-eight hours in 10 per cent KOH solution, or alternatively gently warmed for five minutes in a drop of 10 per cent KOH on a microscope slide. A better mount was obtained if the animal was first killed by trapping it under a cover glass and flooding it with acetic acid in order to fix it in a flat position. After clearing, the specimen was stained in acetic acid fuchsin for twenty-four to forty-eight hours and then dehydrated and mounted in Canada Balsam.

It should be noted here that certain characters that have been used in determinations can be affected by the type of mounting medium, pressure of the cover slip and so on. Such characters are the length and width of the head, width of antennal segments (which also varies with the degree of contraction taking place when the specimen is killed), and width of the cerci in relation to their length.

In no case was it possible to make accurate determinations of immature specimens ; and care should always be taken to ensure that the specimens examined possess the full adult number of legs.

GEOGRAPHICAL DISTRIBUTION

The present survey covers mainly the south-west of England including Cornwall, Devon, Somerset, Dorset, Gloucestershire, Wiltshire, the Isles of Scilly and the Channel Islands, but records from other counties are also included.

Of the genus *Scutigerella*, all the species recorded are quite common over this area with the exception of *S. linsleyi* Michelbacher, which was only found in one place in Devon.

Representatives of the genus *Hanseniella* were only found twice, in a hothouse at Kew and in a glasshouse which had contained tropical plants on the Isles of Scilly. Other European records are also from hothouses and so it seems unlikely that it is an indigenous species.

A specimen of *Neoscutigerella* has only been recorded once, a single damaged example from which the genus was described.

Symphylella species seem to be commoner than those of the other genera, *Symphylella vulgaris* Hansen and *Symphylella isabellae* Silvestri being the

ones most commonly found, while *Symphylella hintoni* sp. n. was found in a number of localities.

Scolopendrella notacantha Gervais was found only in two localities.

Symphylellopsis subnuda Hansen and *Symphylellopsis arvernorum* Ribaut are quite common, but are not as numerous as *Scutigerella* or *Symphylella* species and are often overlooked due to their small size.

KEY TO BRITISH FAMILIES OF SYMPHYLA

1. Paired sense calicles with many setae irregularly distributed around margin of pit. Cerci without stripes or sculpturing near tip. Styli at base of legs well developed. First pair of legs more than half as long as following pair. Length usually more than 4 mm. ..... SCUTIGERELLIDAE Bagnall
–. Paired sense calicles without setae around margin of pit. Cerci with stripes or sculpturing near tip. Styli poorly developed or reduced to slight protuberances. First pair of legs less than half as long as following pair. Length usually less than 4 mm. SCOLOPENDRELLIDAE Bagnall

Family SCUTIGERELLIDAE Bagnall

1913 Scutigerellinae Bagnall, J. Linn. Soc. (Zool.) **32**: 195–199.
1926 Scutigerellidae Attems, *in* Kukenthal, *Handbuch der Zoologie* **4** (1): 11–19.

Head distinctly separated from neck, central rod not interrupted in middle. *Antennae* usually more than 20-segmented, bearing two kinds of setae and sense organs, including a large branched terminal one. *Scuta* simple, not divided into pretergite and metatergite ; intertergal areas between all scuta. Fifteen scuta present, including first which is very reduced ; all others except last with posterior margins rounded or emarginate, but if emarginate, lobes are seldom angular, or if angular are several times broader than long. *Legs* each corresponding with a single scutum except, fourth, sixth and eighth which correspond with two scuta; first pair of legs well developed and more than half length of following pair. Styli well developed and bearing two or more setae*. Calicles with serrated border. *Coxal sacs* eight or nine in number. *Cerci* with smooth terminal area.

KEY TO BRITISH GENERA OF SCUTIGERELLIDAE

1. With a deep cavity beneath middle of posterior end of last scutum, between the cerci ; last scutum more or less emarginate ; antero-lateral setae directed mainly backwards ..... *Scutigerella* Ryder
–. Without a cavity beneath posterior end of last scutum ; last scutum not emarginate ; antero-lateral setae directed mainly forward or laterally ..... 2.
2. All setae on scuta blunt and fusiform except an antero-lateral pair on first scutum ..... *Neoscutigerella* Bagnall
–. All setae on scuta long and pointed, not blunt and fusiform ; antero-lateral setae on most scuta ..... *Hanseniella* Bagnall

* If Ewing's nomenclature (1928) is followed, the second leg consists of coxa, trochanter, femur, tibia and tarsus and paired claw. In this case I consider the missing joint to be the femur.

Genus *SCUTIGERELLA* Ryder

1882 *Scutigerella* Ryder, Proc. U.S. nat. Mus. 5: 234.

Head pyriform ; length and breadth nearly equal ; spiracle opening in the anterior part of each side of the head ; a distinct neck ; a central rod sharply defined at posterior end but less distinct in anterior portion, lateral anterior branches running forward to the base of the antennae, two diagonal thickenings running from base of head to posterior end of post-antennal organs ; main rod interrupted at posterior end by circular area more or less distinct ; dorsal surface of head set with setae mostly short, some long, the longest lying lateral to post-antennal organ. *Antennae* of twenty to fifty segments with two main types of setae ; outer ones thicker and more strongly developed than inner ; setae arranged in whorls ; one whorl on segments nearest head, two on intermediate ones, three or even four on those nearest tip ; small sensory organs and fine sensory hairs present on all segments except first five ; terminal sensory organ present and always stalked. *Scuta* differ in shape, size and degree of emargination of the posterior margin ; third, sixth, ninth, twelfth and fourteenth scuta longer and more emarginate than others; margins of scuta with many short and fewer longer outstanding marginal and sub-marginal setae which vary in length and number ; antero-lateral setae usually present on anterior scuta ; last scutum of different shape to others, with only a very slight emargination in centre overlying cavity between cerci ; no more than two setae in cavity between cerci. *Legs* with intricate patterns of sculpturing on some segments and densely setose ; setae on outer dorsal surface of legs much longer than those on inner ventral surface ; first pair of legs with one segment less than following pair, and sparsely clothed with setae, some long, the longest one lying on the inner surface of the trochanter (in *Scutigerella lineatus* this is replaced by a peg-like outgrowth). Styli present on last ten pairs of legs and each bearing two to three setae. *Coxal sacs* usually eight in number on legs three to ten. *Cerci* densely clothed with setae nearly to tip and terminating in long and short setae with opening of silk gland between them. *Length* 2·5–8·3 mm.

Taxonomic features

It is important to note that accurate determinations can only be made on mature adult specimens. The instar of a specimen of this genus can be estimated from the shape of the penultimate scutum, which has a smooth posterior margin when mature, but an irregularly scalloped one when immature (see Michelbacher, 1938, 1942).

All species of the genus have many variable characters, and, as most species have been described from a few specimens taken in a single locality, the range of variation in many species has not yet been defined. In addition distortion can be caused by the mounting technique used.

The length of the head, the length of the setae lying between the post-antennal organ and the spiracle, and the number of segments in unbroken antennae all offer good specific characters. The length/width ratio of the head, its shape, and the width of the third antennal segment, have all been

used by Michelbacher and Hansen. These are not reliable characters however as they can vary with the mounting technique.

The best specific characters appear to be the shape and size of the dorsal scuta. The first six and the last scuta have been described here. The greatest specific differences are found in the second and sixth scuta. The difference in number of marginal and submarginal setae is not a good character, since the variation in number within a species may overlap with that of other species. The length of the long outstanding, marginal and submarginal setae in relation to that of the short setae does show good specific variation. Long outstanding setae are present on the second scutum of all species described at present, but the number of scuta on which these setae can be distinguished varies with the species. The shape of the last scutum and the cavity beneath it, is of some taxonomic value, but shows a little variation and may be distorted in mounting. There are two setae in this cavity, which vary considerably in length in different species. The shape of the cercus is a slightly variable character and the length/width ratio of the cercus can be affected by pressure. The length of the long fine seta at the end of the cercus, measured from notch to tip, and the amount of expansion at the end of the cercus provide good specific characters. The relative dimensions of the segments of the legs are too variable to be good characters, but the density of their setae, particularly that of the first pair, is a good character. The first pair of legs of two species (one British) bear a peg-like projection on the inner surface of the trochanter. The number of coxal sacs, the shape and number of setae borne on the last two coxal sacs, and the body length measured from front of head to tip of cercus all show good specific differences.

KEY TO BRITISH SPECIES OF SCUTIGERELLA

1. Posterior margin of second scutum strongly emarginate..... 2.

–. Posterior margin of second scutum slightly emarginate, almost linear ..... 4.

2. Coxal plates corresponding with last pair of legs, with no setae; scuta very deeply emarginate, legs sparsely setose, very small species less than 5 mm. long ..... *S. linsleyi* Michelbacher

–. Coxal plates corresponding with last pair of legs with at least one seta, usually two or more ; scuta not so deeply emarginate ; legs densely setose, larger species usually more than 5 mm. long 3.

3. Long outstanding antero-lateral setae on nearly all scuta; 2nd scutum only very moderately emarginate ; cavity beneath last scutum usually V-shaped and with fewer long setae overlying it *S. palmonii* Michelbacher

–. Antero-lateral setae not so long and outstanding, not present on posterior scuta ; second scutum more deeply emarginate ; cavity beneath last scutum broadly U-shaped with many short setae overlying it ..... *S. immaculata* Newport

4. Small species less than 4·8 mm. long ; setae sparse and short ; male with peg-like projection on inner surface of trochanter of first leg ..... *S. lineatus* sp. n.

–. Large species more than 5·1 mm. long ; setae longer and numerous ; no peg-like projection on first leg in either sex.... *S. causeyae* Michelbacher

SCUTIGERELLA IMMACULATA Newport

1845 *Scolopendrella immaculata* Newport, Trans. Linn. Soc. Lond. (Zool.) **19**: 373.
1873 *Scolopendrella americana* Packard, Proc. Boston Soc. nat. Hist. **16**: 111.
1882 *Scutigerella immaculata* Ryder, Proc. U.S. nat. Mus. **5**: 234.
1905 *Scutigerella californica* Woodworth, Calif. J. Tech. **6**: 38.
1914 *Scutigerella biscutata* Bagnall, Trans. nat. Hist. Soc. Northumb. **4**: 17.
1914 *Scutigerella spinipes* Bagnall, ibid. **4**: 17.

Adult : Length 5·5–7·0 mm. *Head* (Fig. 1f) with setae mostly short, 0·017–0·067 mm. long ; longest seta post-antennal, 0·056–0·067 mm. long. *Antenna* of twenty-six to thirty-four segments, usually thirty segmented. *Scuta* (Fig. 1a–e) moderately emarginate posteriorly ; long marginal and submarginal setae seldom more than twice as long as corresponding short setae ; long setae becoming progressively shorter posteriorly and not distinguishable from the short, after the sixth or seventh scutum (see Table) ; last scutum (Fig. 1g) usually only shallowly emarginate in centre, with a large number of

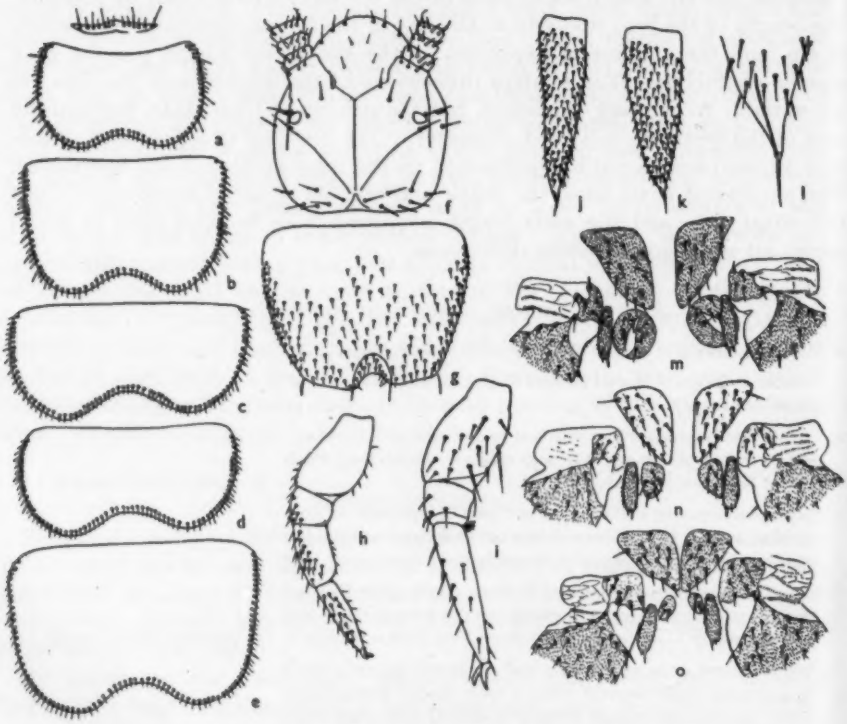

Fig. 1.—*Scutigerella immaculata* Newport.

a–e, first to sixth dorsal scuta ; f, dorsal view of head ; g, last dorsal scutum ; h, posterior view of last leg of left side ; i, posterior view of first leg of left side ; j, dorsal view of right cercus ; k, alternative type of right cercus ; l, tip of cercus ; m–o, ventral view of bases of last three pairs of legs. All ×72 except i and l which are ×190 and m–o which are ×140.

setae overlying U-shaped cavity ; setae in cavity quite short. *Legs* densely clothed with setae. Styli (Fig. 1m) each with two setae only. *Coxal plates* (Fig. 1m–o) of last pair of legs each with two to three setae ; those of penultimate pair with four to six setae. *Cerci* (Fig. 1 j, k) densely clothed with short setae and with terminal area moderately expanded ; apical seta short 0·038–0·047 mm. long.

Chaetotaxy

1. Dorsal scuta (based on sixty-two adult specimens from seventeen localities).

	Total No. of marginal setae	No. of long marginal setae	Width of scutum (mm.)	Length of antero-lateral seta (mm.)
Second scutum	48–61	6–8	0·35–0·39	0·046–0·049
Third scutum	64–74	8–10	0·41–0·48	0·042–0·046
Fourth scutum	60–70	6–8	0·46–0·53	0·035–0·042
Fifth scutum	58–68	6–8	0·42–0·49	0·032–0·035
Sixth scutum	70–96	6–8	0·49–0·56	0·028–0·035

2. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	5–6	2–4	3–4	4–6	16–17
Tibia	1–2	0	0	2–3	4
Trochanter	0–1	2–3	0	9–10	13–14

3. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	6–7	6–7	15–19	13–16	43–48
Tibia	5–6	4–5	16–20	14–17	40–46
Femur	3–4	0	9–11	4–8	36–40
Trochanter	3–4	5–7	28–35	1	37–40

Type : Once deposited in the British Museum (Natural History), now apparently lost. Type locality ; St. John's Wood, London. The present description is based on specimens from Jersey, Channel Isles.

Distribution : Cosmopolitan. Recorded previously in Britain from Scotland, Ireland, Durham, Yorkshire, and Cheshire. In addition I have found it in Gloucestershire, Somerset, Wiltshire, Dorset, Devon, Cornwall, the Isles of Scilly and the Channel Isles.

Comparative notes: *S. immaculata* is most closely related to *S. silvestri* Mich. from which it may be distinguished by the presence of two setae instead of three on the styli and the much shorter cerci. *S. silvestri* is also longer.

Hansen (1903) claims there are nineteen to fifty antennal segments, but his specimens with few segments were probably immature, and those with many belonged to other species. Michelbacher (1942) figures no long setae on the fourth scutum, but such setae are present on specimens named by him and deposited in the British Museum (Natural History). In his key he uses the number of marginal and sub-marginal setae on the second scutum as a diagnostic character, *S. immaculata* and *S. silvestri* having more than fifty-two such setae. In fact some of his specimens only possess fifty such setae and some British specimens as few as forty-eight. The principal diagnostic features of *S. immaculata* are the numerous short setae over the body and the rounded deeply emarginate scuta.

Scolopendrella americana Packard and *Scutigerella californica* Woodworth are synonyms of *S. immaculata*, as shown by Michelbacher (1942). *Scutigerella*

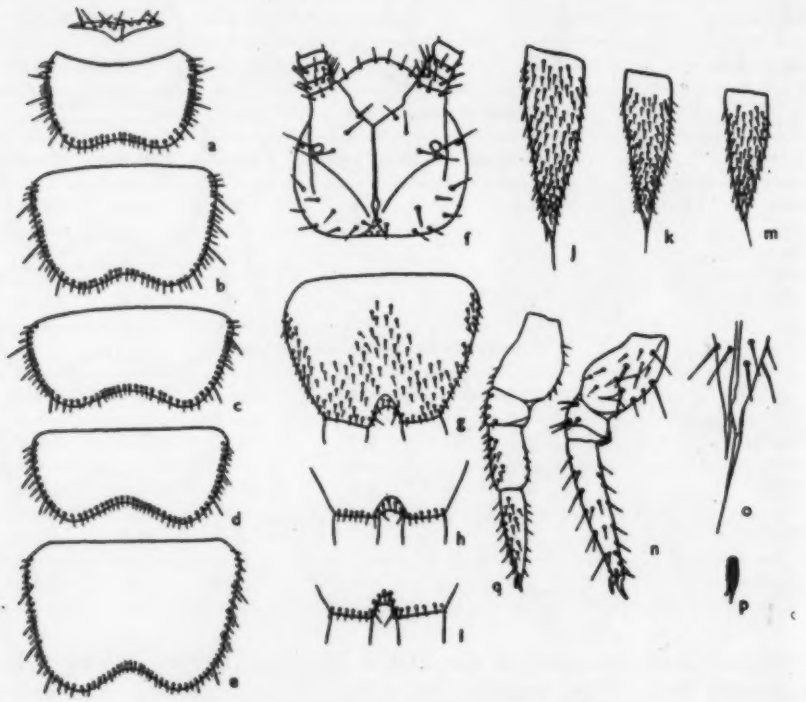

Fig. 2.—*Scutigerella palmonii* Michelbacher.

a–e, first to sixth dorsal scuta; f, dorsal view of head; g, last dorsal scutum; h–i, alternative shapes of cavity below last scutum; j–m, dorsal view of right cercus (with alternative types); n, posterior view of first leg of left side; o, tip of cercus; p, typical stylus; q, posterior view of last leg of left side. All ×72 except n and o which are ×190.

biscutata Bagnall and *Scutigerella spinipes* Bagnall are fifth and seventh instar individuals of *S. immaculata* respectively, as is evident from the descriptions and from an examination of topotypes of these species in the British Museum.

Habits : *S. immaculata* can most easily be found around the roots of growing plants on which it feeds, particularly in moist soil. It is commonly a pest of cultivated crops, but it may also be found under stones, in forest litter and at considerable depths in the soil.

SCUTIGERELLA PALMONII Michelbacher

1942 Ann. ent. Soc. Amer. **35**: 274.

Adult : length 4·1–7·0 mm. *Head* (Fig. 2 f) with setae mostly short, some very long 0·017–0·088 mm. long ; longest seta post-antennal 0·067–0·088 mm. long. *Antenna* of twenty-seven to forty-three segments usually thirty-seven segmented. *Scuta* (Fig. 2 a–e) with second scutum slightly emarginate, others moderately emarginate, lateral margins relatively straight ; long marginal and submarginal setae inset from the margin and very conspicuous, usually two or three times as long as corresponding short setae ; long setae present on almost all scuta ; last scutum (Fig. 2 g) with moderately deep median emargination overlying V-shaped cavity containing two long setae ; never more than eight setae around the border of this emargination. Styli each with two setae only. *Coxal plates* of last pair of legs each with one to three setae and those of penultimate pair with four to six setae. *Cerci* (Fig. 2 j–m) densely clothed with setae ; little expansion of terminal area ; apical seta long 0·055–0·070 mm. in length.

Chaetotaxy

1. Dorsal scuta (based on forty-four specimens from fifteen localities).

	Total No. of marginal setae	No. of long marginal setae	Width of scutum (mm.)	Length of antero-lateral seta (mm.)
Second scutum	36–50	6–8	0·24–0·42	0·06–0·067
Third scutum	45–66	6–10	0·38–0·56	0·06–0·067
Fourth scutum	46–62	6–8	0·44–0·63	0·056–0·063
Fifth scutum	45–64	4–6	0·42–0·60	0·049–0·053
Sixth scutum	68–86	10–12	0·50–0·67	0·049–0·053

2. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	6	5–7	5–7	6–8	24–27
Tibia	2–3	0	0–1	3	5–6
Trochanter	0	2–3	0	12–15	14–17

3. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	6–8	7–10	10–17	16–32	39–66
Tibia	6–8	4–5	16–33	9–20	36–67
Femur	4–5	0	9–12	1–4	17–22
Trochanter	2–3	6–8	32–42	0	42–49

Type : In the collection of the University of California, No. 5191. Type locality : banks of River Jordan, Palestine. The present description is based on specimens from Cheddar, Somerset.

Distribution : Previously recorded only from the type locality. I have found it in eight localities in Somerset, two in Dorset, four in Devon and one in Lancashire.

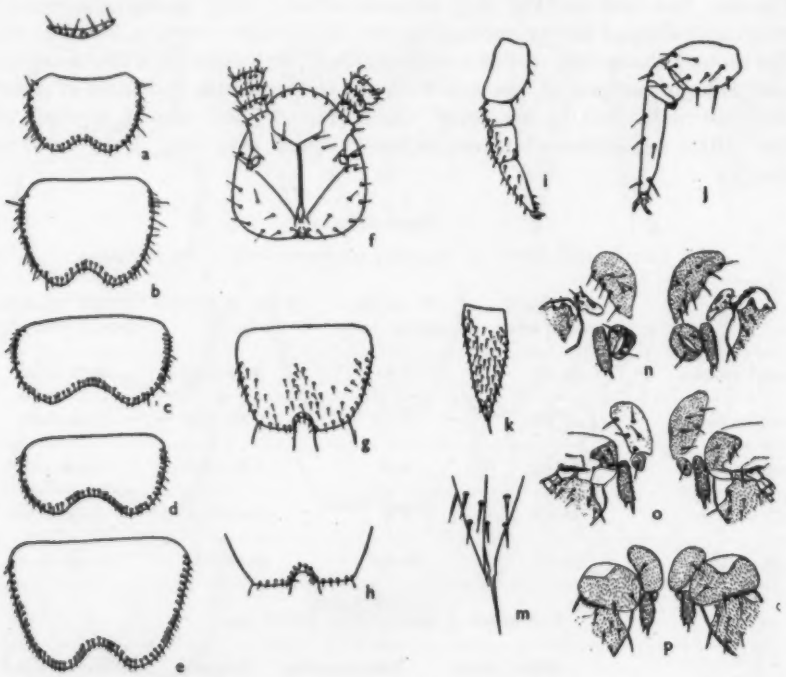

Fig. 3.—*Scutigerella linsleyi* Michelbacher.

a–e, first to sixth dorsal scuta ; f, dorsal view of head ; g, last scutum ; h, alternative shape of cavity below last scutum ; i, posterior view of last leg of left side ; j, posterior view of first leg of left side ; k, dorsal view of right cercus ; m, tip of cercus ; n–p, ventral view of bases of last three pairs of legs. All ×72 except j and m which are ×190, and n–p which are ×140.

Comparative notes : *S. palmonii* is most closely related to *S. immaculata*, from which it may be distinguished by the presence of certain longer setae, particularly the post-antennal seta, the antero-lateral seta, those at the tips of the cerci, and those in the cavity below the last scutum. This cavity is much more V-shaped than that of *S. immaculata*, the posterior margins of the scuta are less emarginate, the head is broader and more angled at the sides and the cerci are more pointed.

Habits : *S. palmonii* is found in identical situations to *S. immaculata* and also attacks a wide range of plants with succulent root systems.

SCUTIGERELLA LINSLEYI Michelbacher

1942 Ann. ent. Soc. Amer. **35**: 283.

Adult : Length 3·5–4·9 mm. *Head* (Fig. 3 f) with setae, mostly short, some longer 0·014–0·063 mm. long. *Antenna* of twenty to twenty-four segments, usually twenty-two segmented. *Scuta* (Fig. 3 a–e) very strongly emarginate posteriorly, lateral margins rounded ; long marginal and submarginal setae never more than twice as long as the corresponding short ones ; these long setae becoming progressively shorter posteriorly (see Table) and not distinguishable from short setae after fifth or six scutum. Last scutum (Fig. 3 g) deeply emarginate, overlying broadly U-shaped cavity ; setae in cavity short. Styli (Fig. 3 n–p) each with two setae only. *Coxal plates* (Fig. 3 n–p) of last pair of legs very small and bearing no setae ; those of penultimate pair only slightly larger and each bearing only one seta. *Cerci* (Fig. 3 k–m) short and densely clothed with setae ; terminal area not expanded ; apical seta short 0·39 mm. long.

Chaetotaxy

1. Dorsal scuta (based on four specimens from one locality).

	Total No. of marginal setae	No. of long marginal setae	Width of scutum (mm.)	Length of antero-lateral seta (mm.)
Second scutum	33–42	6–8	0·28–0·29	0·045
Third scutum	40–50	6–8	0·35–0·36	0·038
Fourth scutum	40–52	6–8	0·40–0·41	0·035
Fifth scutum	40–46	4	0·38–0·39	0·026
Sixth scutum	56–62	0	0·42–0·43	0·025

2. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	3–4	2–3	2–4	1–2	9–11
Tibia	1	0	0	2	2
Trochantér	0	3	0	6–7	9–10

3. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	4–5	3–4	4–7	4–5	16–19
Tibia	4	0–1	3–7	5–7	13–16
Femur	2–3	0	3–5	1	7–9
Trochanter	0	1–5	10–16	0	13–17

Type : In the collection of the University of California, No. 5194. Type locality : Idyllwild, California. The present description is based on specimens from Bishopsteignton, Devon.

Distribution : Recorded previously only from the type locality. I have only found it in one locality, Bishopsteignton, Devon.

Comparative notes : *S. linsleyi* is most closely related to *S. immaculata*, from which it may be distinguished by its small size, deep emargination of the

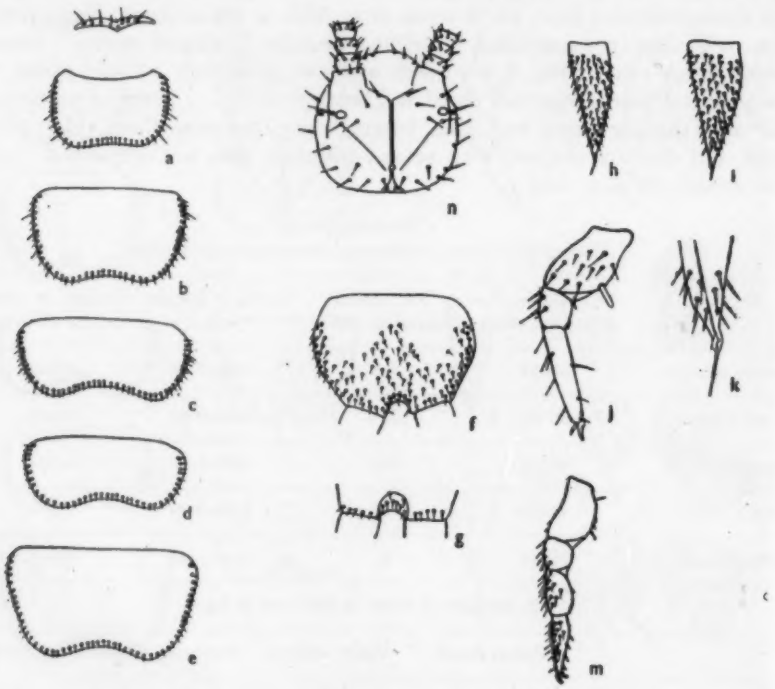

Fig. 4.—*Scutigerella lineatus*, sp. n.

a–e, first to sixth dorsal scuta ; f, last scutum ; g, alternative shape of cavity below last scutum ; h–i, dorsal view of two types of right cercus ; j, posterior view of first leg of left side of male ; k, tip of cercus ; m, posterior view of last leg of left side ; n, dorsal view of head. All ×72 except j and k which are ×180.

posterior margin of the scuta and few setae on the posterior coxal plates. In addition it is distinctive in having not more than twenty-four antennal segments, and relatively sparse setae on the scuta and legs.

Habits : It was found in the upper layers of the soil in extremely large numbers causing considerable damage to the roots of cabbage plants.

SCUTIGERELLA LINEATUS sp. n.

Adult : Length 2·8–4·8 mm. *Head* (Fig. 4 n) with setae, mostly short, some long 0·014–0·049 mm. long. *Antenna* of twenty-two to thirty-two segments, usually twenty-eight segmented. Scuta (Fig. 4 a–e) with posterior margin of second scutum almost linear, others only slightly emarginate posteriorly ; long marginal and submarginal setae usually less than twice as long as corresponding short setae ; long setae becoming progressively shorter posteriorly and not distinguishable from the short after fifth or sixth scutum (see Table) ; last scutum (Fig. 4 f) only moderately emarginate and overlying broad U-shaped cavity ; setae in cavity short. *Coxal plates* of last pair of legs each with one seta only ; those of penultimate pair each with one to four setae. Styli each with two setae only. *Cerci* (Fig. 4 h–i) short, densely clothed with short setae and with terminal area moderately expanded ; apical seta short 0·039–0·049 mm. long.

Chaetotaxy

1. Dorsal scuta (based on fourteen adult specimens from five localities).

	Total No. of marginal setae	No. of long marginal setae	Width of scutum (mm.)	Length of antero-lateral seta (mm.)
Second scutum	36–42	6	0·23–0·29	0·035–0·042
Third scutum	46–56	6–8	0·29–0·40	0·034–0·039
Fourth scutum	42–50	4	0·33–0·43	0·026–0·030
Fifth scutum	40–50	4	0·31–0·40	0·024–0·028
Sixth scutum	50–60	0	0·37–0·46	0·021–0·024

2. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	4–7	1–4	2–4	5–7	15–20
Tibia	2	0	2	1–2	5–6
Trochanter	0–1	0(P)	9–12	0	9–12

3. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	4–7	4–5	10–12	12–15	32–36
Tibia	4–6	1–4	8–10	12–16	27–32
Femur	3–4	0	4–6	4–5	12–14
Trochanter	2–3	2–5	18–22	0	25–28

Type : Deposited in British Museum. Type locality : Cheddar Valley Nurseries, Cheddar, Somerset.

Distribution : Bath, Cheddar, Draycott, and Langford in Somerset. South Tawton in Devon.

Comparative notes : *S. lineatus* is most closely related to *S. armata* Hansen, a species only recorded from Algeria, and which is characterized by a peg-like projection on the inner surface of the trochanter of the first leg, in the same position as a very long seta in other species. *S. lineatus* has a similar structure on the first leg, but in this species it is found only in the male. The species may also be distinguished from *S. armata* by the much more linear posterior margins of the scuta and the much shorter cerci. The scuta have a rather similar shape to *S. causeyae* Michelbacher but this is a very much smaller species.

Habits : It has been found for the most part in cultivated soils, particularly in greenhouses, feeding on growing plant roots.

SCUTIGERELLA CAUSEYAE Michelbacher

1942 Ann. ent. Soc. Amer. **35**: 280.

Adult : length 5·1–8·2 mm. *Head* (Fig. 5 f) broad, with setae mostly short, some very long 0·021–0·080 mm. long ; longest seta post-antennal 0·080–0·105 mm. long. *Antenna* of twenty-eight to thirty-nine segments usually thirty segmented. *Scuta* (Fig. 5 a–e) particularly the second, only very slightly emarginate; long marginal and submarginal setae, slightly inset from the margin and more than three times as long as the corresponding short setae ; long setae becoming progressively shorter posteriorly, not distinguishable from the short after the fifth or sixth scutum ; last scutum (Fig. 5 g) usually with only a shallow median emargination, and with numerous setae overlying a broadly U-shaped cavity ; setae in cavity quite short. *Coxal plates* of last pair of legs each with one to two setae ; those of penultimate pair with four to six setae. Styli each with two setae only. *Cerci* (Fig. 5 k) large and densely clothed with short setae ; terminal area strongly expanded ; apical setae long 0·046–0·056 mm. long.

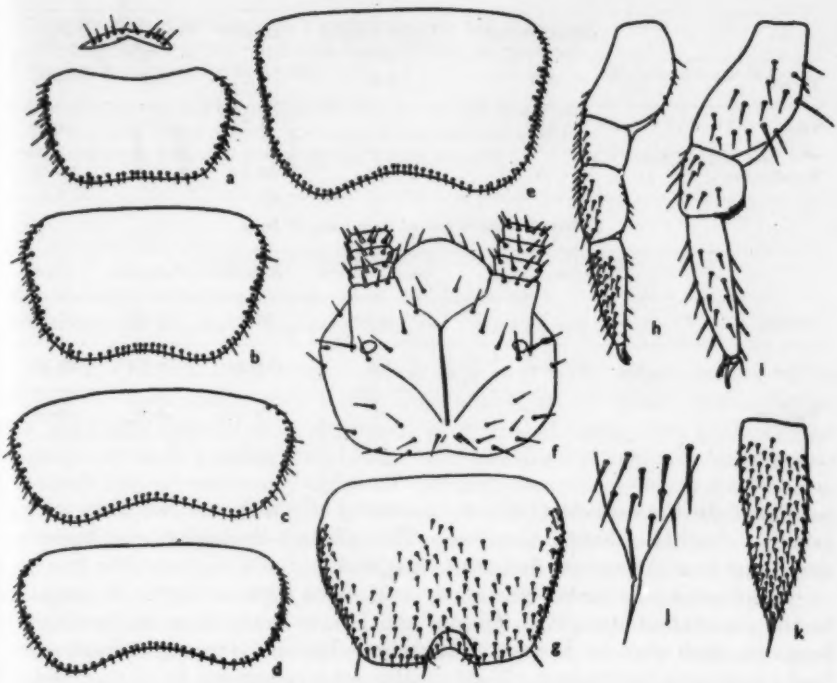

Fig. 5.—*Scutigerella causeyae* Michelbacher.

a–e, first to sixth dorsal scuta ; f, dorsal view of head ; g, last scutum ; h, posterior view of last leg of left side ; i, posterior view of first leg of left side ; j, tip of right cercus ; k, dorsal view of right cercus. All ×72 except i and j which are ×180.

Chaetotaxy

1. Dorsal scuta (based on twenty-three specimens from fifteen localities).

	Total No. of marginal setae	No. of long marginal setae	Width of scutum (mm.)	Length of antero-lateral seta (mm.)
Second scutum	38–48	6–8	0·42–0·49	0·053–0·060
Third scutum	54–68	6–8	0·52–0·62	0·053–0·056
Fourth scutum	48–62	6	0·62–0·69	0·046–0·049
Fifth scutum	48–54	4–6	0·60–0·67	0·042–0·046
Sixth scutum	64–82	6–8	0·69–0·79	0·035–0·039

2. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	4–7	4–6	4–7	4–10	18–26
Tibia	2–4	0	4–7	0	8–10
Trochanter	0	3–4	14–18	0	17–23

3. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	5–10	6–10	23–54	22–36	56–106
Tibia	4–6	3–4	12–28	10–24	32–64
Femur	2–4	0	8–18	6–8	14–30
Trochanter	0–4	3–5	26–52	0	30–56

Type : In the collection of the University of California No. 5193. Type locality : Durham, North Carolina. The present description is based on specimens from Draycott, Somerset, England.

Distribution : Recorded previously only from type locality. It seems to be the commonest species in Britain, and I have found it in six localities in Somerset and also in Dorset, Hampshire, Devon, Surrey, Leicestershire, Derbyshire and Lancashire. I have also seen specimens from Cumberland and Ireland.

Comparative notes : *S. causeyae* Michelbacher is most closely related to *S. verhoeffi* Michelbacher from which it may be distinguished by the possession of eight pairs of coxal sacs instead of nine and the U-shaped cavity beneath the last scutum instead of a strongly V-shaped one in *S. verhoeffi*. All the British specimens found and in addition some from Sweden, had more numerous setae and were of a much larger size than those of the other species.

Habits: This species appears to be most common in forest litter and soils containing a high proportion of organic matter.

Genus *HANSENIELLA* Bagnall

1913 *Hansenicella* Bagnall, J. Linn. Soc. (Zool.) **32**, 197.

Head rounded with central rod only distinct in middle, not continuous through entire length and without anterior branches ; no diagonal sutures ; dorsal surface with some long setae on anterior portion, longest seta not post-antennal. *Antenna* of twenty to forty-five segments with only stout setae present. *Scuta* : first two and last scuta with rounded posterior margins, others emarginate ; long outstanding antero-lateral setae on scuta 2, 3, 4, 6, 7 and 9 ; directed forward on first two scuta. No cavity present under last scutum between cerci. *Legs* densely setose, setae on dorsal surface of tarsus not appreciably longer than those on ventral surface. *Coxal Sacs* only fully developed on legs 3 to 9. Styli long and narrow with two long terminal setae and sometimes additional ones. *Cerci* with elongated terminal area.

KEY TO BRITISH SPECIES OF *HANSENIELLA*

1. Posterior claw of last leg strongly curved and only half as long as anterior claw ; primary whorl of antennal setae on eleventh segment as long ventrally as dorsally ..... *H. unguiculata* Hansen

–. Posterior claw of last leg only moderately curved and more than half as long as anterior claw ; primary whorl of antennal setae on eleventh segment much shorter ventrally than dorsally ..... *H. caldaria* Hansen

HANSENIELLA UNGUICULATA Hansen

1904 *Scutigerella unguiculata* Hansen, Quart. J. micr. Sci. **47**: 1.

1913 *Hanseniella unguiculata* Bagnall, J. Linn. Soc. (Zool.) **32**: 197.

Adult : Length 3·0–3·6 mm. *Head* (Fig. 6 g) with setae, mostly short 0·010–0·037 mm. long ; with a few longer at front of head ; post-antennal seta not longer than others. *Antenna* (Fig. 6 p–q) of twenty-two to thirty-four segments, setae in primary whorl long, both dorsally and ventrally on segments of distal half of antenna ; those of eleventh segment ±0·034 mm. above, 0·031 mm. below. *Scuta* (Fig. 6 a–f) ; second, third and last scuta with rounded posterior margins, other scuta slightly emarginate ; antero-lateral setae very long and outstanding, directed forwards on first two segments and backwards on segments 4, 6, 7 and 9 ; these setae much shorter on other segments ; no cavity beneath last scutum. *Legs* (Fig. 6 m–n) with anterior claw of last pair of legs very long and robust, posterior claw very curved, only half as long as anterior ; first pair of legs with posterior claw very small and slender. *Coxal sacs* fully developed at bases of third to ninth pairs of legs, with only rudimentary plates at bases of tenth and eleventh pairs, completely absent on twelfth pair. Styli (Fig. 6 c) large, with two long setae. *Cerci* (Fig. 6 j) densely clothed with short setae ; terminal area long and narrow, as long as apical seta.

Chaetotaxy

1. Dorsal scuta (based on ten adult specimens from two localities).

No. of scutum	Total No. of marginal setae	Width of scutum (mm.)
Second scutum	30–34	0·23–0·27
Third scutum	38–42	0·33–0·42
Fourth scutum	40–44	0·42–0·50
Fifth scutum	40–44	0·42–0·48
Sixth scutum	44–50	0·47–0·53

2. Length of antero-lateral setae.

No. of scutum	Length of seta (mm.)	No. of scutum	Length of seta (mm.)
Second scutum	0·073–0·081	Eighth scutum	0·035–0·042
Third scutum	0·073–0·081	Ninth scutum	0·073–0·081
Fourth scutum	0·073–0·081	Tenth scutum	0·031–0·038
Fifth scutum	0·035–0·042	Eleventh scutum	0·024–0·032
Sixth scutum	0·073–0·081	Twelfth scutum	0·028–0·035
Seventh scutum	0·073–0·081	Thirteenth scutum	0·024–0·032

3. Number of setae on first pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	3–5	2–3	3–7	3–4	12–16
Tibia	2	0	3–4	0	5–6
Trochanter	0	1–2	13–17	0	4–18

4. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	5–7	5–6	9–12	8–12	29–35
Tibia	5–7	3–4	16–19	9–13	36–40
Femur	3	0	9–11	2–5	14–17
Trochanter	1–2	5–8	29–33	0	38–41

Type : In Copenhagen Museum. Type locality : La Moka, Venezuela. This description is based on specimens from Kew Gardens, London.

Distribution : This species has previously been known only from the type locality. I have found it in Britain in a tropical house at Kew and a hothouse at Tresco, Isles of Scilly.

Comparative notes : *H. unguiculata* is most closely related to *H. subunguiculata* Imms from which it may be distinguished by the greater emargination of the posterior margin of the penultimate scutum, and the greater length of the posterior claw of the last pair of legs. It is also closely related to *H. caldaria* Hansen. The cerci are shorter here than in Hansen's original description, but this is a variable character in many species of Symphyla.

Habits : This species has only been found in this country in hothouses and it has probably been introduced among the roots of tropical plants. Nearly

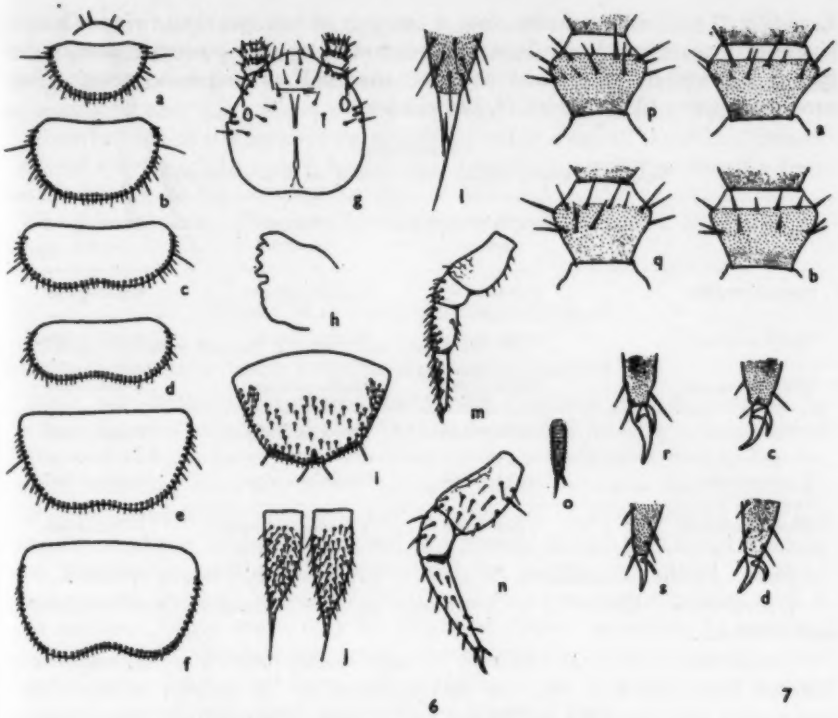

Fig. 6.—*Hanseniella unguiculata* Hansen.

a–f, first to seventh dorsal scuta ; g, dorsal view of head ; h, right mandible ; i, last dorsal scutum; j, right cercus from side and above ; l, tip of cercus ; m, posterior view of last leg of left side ; n, posterior view of first leg of left side ; o, typical stylus ; p, eleventh antennal segment, dorsal view ; q, eleventh antennal segment, ventral view ; r, dorsal view of claw of last leg of right side ; s, dorsal view of claw of first leg of right side.

Fig. 7.—*Hanseniella caldaria* Hansen.

a, eleventh antennal segment, dorsal view ; b, eleventh antennal segment, ventral view ; c, dorsal view of claw of last leg of right side ; d, dorsal view of claw of first leg of right side. All ×72 except 6 l, n & o, which are ×180 and 6 p–s, and 7a–d which are ×316.

all the species of the genus *Hanseniella* are tropical. It is not known whether it is a primary plant feeder, but the weak teeth on the mandibles indicate that this is not the case.

HANSENIELLA CALDARIA Hansen

1904 *Scutigerella caldaria* Hansen, Quart. J. micr. Sci. **47**: 1.
1913 *Hanseniella caldaria* Bagnall, J. Linn. Soc, (Zool.) **32**: 197.

Adult: Length 2·8–4·0 mm. *Head* as in *H. unguiculata*. *Antenna* (Fig. 7 a–b) of twenty-three to twenty-eight segments ; primary whorl of antennal setae much shorter ventrally than dorsally, those of eleventh segment about 0·038 mm. dorsally 0·021 mm. ventrally. *Scuta* shaped as those of *H. unguiculata*, but antero-lateral setae longer and distinguishable even on the penultimate scutum.

Legs (Fig. 7 c–d) with anterior claw of last pair of legs less than twice as long as posterior ; posterior claw robust and not very curved ; posterior claw of first pair of legs well-developed and not more than half as long as anterior. *Coxal sacs*, styli, *Cerci* like those of *H. unguiculata*.

Chaetotaxy

Length of antero-lateral setae (based on five specimens).

No. of scutum	Length of seta (mm.)	No. of scutum	Length of seta (mm.)
Second scutum	0·084–0·088	Eighth scutum	0·052–0·060
Third scutum	0·084–0·088	Ninth scutum	0·084–0·088
Fourth scutum	0·084–0·088	Tenth scutum	0·056–0·063
Fifth scutum	0·052–0·060	Eleventh scutum	0·052–0·060
Sixth scutum	0·084–0·088	Twelfth scutum	0·060–0·067
Seventh scutum	0·084–0·088	Thirteenth scutum	0·052–0·060

Type : In the Copenhagen Museum. Type locality : South America.

Distribution : Recorded in hothouses in Kew, Glasgow, Northumberland and Durham.

Comparative notes : *H. caldaria* is most closely related to *H. unguiculata* Hansen from which it may be distinguished by its shorter anterior claw, less curved posterior claw on the last pair of legs ; the relatively large posterior claw on the first pair of legs ; and the antennal setae which are shorter on the ventral surface than the dorsal surface. The antero-lateral setae of scuta 2, 3, 4, 6, 7 and 9 are longer, but less than twice as long as those of other scuta, whereas in *H. unguiculata* they are shorter but at least twice as long as those on other scuta.

Habits : Its habits are similar to those of *H. unguiculata*.

Genus *NEOSCUTIGERELLA* Bagnall

1911 *Neoscutigerella* Bagnall, J. Linn. Soc. (Zool.) **32**: 197.

Head : rounded. *Scuta* with posterior margin emarginate or only slightly rounded ; with a long antero-lateral seta on second scutum, which may also be present on other scuta ; all setae on scuta with exception of antero-laterals, short and blunt. *Cerci* short ; with long stiff setae ; long and narrow terminal area.

NEOSCUTIGERELLA HANSENI Bagnall

1911 *Scutigerella hanseni* Bagnall, Trans. nat. Hist. Soc. Northumb. **4**: 17.
1913 *Neoscutigerella hanseni* Bagnall, J. Linn. Soc. (Zool.) **32**: 197.

Adult : Length 4·65 mm. *Head* rounded, dorsal surface with setae mostly characteristically short, blunt, and fusiform in posterior half ; some long and slender in anterior half. Antennae long, thirty-eight segmented, setae stout and of only one type, not longer on inner surface than on outer.

Scuta, first two only slightly emarginate, outstanding antero-lateral setae on second scutum only ; all other setae short, blunt and broad in the middle. *Legs* strongly setose, some setae being short and blunt as those on the scuta, but majority long and thin. *Cerci* with a moderate number of long stiff setae.

Distribution : A single specimen was described by Bagnall from Co. Durham. A second species of the genus, based on a unique specimen has recently been described from Madagascar by Aubry and Masson.

Comparative notes : The short blunt setae easily distinguish it from all other species.

Family SCOLOPENDRELLIDAE Bagnall

1913 Scolopendrellidae Bagnall, J. Linn. Soc. (Zool.) **32**: 195.
1926 Scolopendrellidae Attems, *in* Kukenthal *Handbuch der Zoologie* **4**: 11.

Head not distinctly separated from neck ; central rod interrupted in middle. *Antenna* usually less than twenty segmented, bearing only one kind of seta and some sense organs. *Scuta* complex, seventeen to twenty-four in number, including first, which may be very reduced or quite well-developed ; some scuta divided into pretergite and metatergite ; if lobes present they are triangular in shape, longer than broad and present on thirteen scuta ; in one genus (*Geophilella*), scuta only represented by paired oval plates. *Calicles* with a smooth border. *Legs* 4, 6, 8, 10 and 12 never corresponding with a single scutum ; other scuta may be single or double according to species ; first pair of legs moderately developed, never more than half the length of the following pair. Styli poorly developed or rudimentary. *Coxal Sacs* never more than seven in number. *Cerci* with striated terminal area.

KEY TO BRITISH GENERA OF SCOLOPENDRELLIDAE

1. Twenty-one or twenty-two poorly defined dorsal scuta, first relatively well-developed. Cerci short with long conical terminal area ..... *Symphylellopsis* Ribaut
–. Only seventeen dorsal scuta, first represented only by setae. Cerci long with small expanded terminal area ..... 2.
2. First pair of legs relatively well-developed. Posterior margins of scuta between projections with transverse belt of longitudinal striae ..... *Scolopendrella* Gervais
–. First pair of legs vestigial, only represented by slight swelling behind head. Posterior margins of scuta without transverse belts of longitudinal striae ..... *Symphylella* Silvestri

Genus *SYMPHYLELLOPSIS* Ribaut

1931 *Symphylellopsis* Ribaut, Bull. Soc. Hist. nat. Toulouse **46**: 463.

Head oval, elongate, longer than broad, with central rod only distinct in posterior portion, broken in middle without lateral branches and barely visible in anterior portion ; spiracles opening at sides of head slightly posteriorly. Post-antennal organ indistinct ; opening to exterior by narrow tube. Dorsal surface of head set with short setae. *Antennae* of less than twenty segments with only small short setae, particularly on distal segments ; only main whorls of

setae and weak subsidiary whorls present. *Scuta* twenty-one or twenty-two in number ; thirteen of these with paired processes considerably longer than broad ; first scutum relatively well-developed with diagonal thickenings ; those scuta corresponding with legs 5, 7, 9, 11 and 12 (and sometimes 3) double, and separated by only a simple suture ; other paired scuta separated by an intertergal zone. *Legs* very short, first pair fairly well-developed with three movable joints ; not more than half as long as following pair. Styli rudimentary. *Coxal Sacs* not well-developed, seven in number, present at base of legs 3–9. *Cerci* short, without honeycomb structure, not more than four times as long as wide ; sparsely setose and with large conical terminal area, striated and with ring of setae around terminal area, ending with large single apical seta.

Key to British species of *Symphylellopsis*

1. Third pair of legs corresponding with a single scutum; first scutum short ; posterior projections of scuta narrow and considerably farther apart than their length ..... *S. subnuda* Hansen

–. Third pair of legs corresponding with a double scutum ; first scutum longer ; posterior projections of scuta broader and about the same distance apart as their length ..... *S. arvernorum* Ribaut

Symphylellopsis subnuda Hansen

1903 *Scolopendrella subnuda* Hansen, Quart. J. micr. Sci. **47**: 1.

1913 *Scolopendrellopsis subnuda* Bagnall, J. Linn. Soc. (Zool.) **32**: 197.

1931 *Symphylellopsis subnuda* Ribaut, Bull. Soc. Hist. nat. Toulouse **62**: 463.

Adult : Length 1·2–2·0 mm. *Head* oval with sparse short setae 0·005–0·01 mm. long ; post-antennal organ with distinct tube opening to exterior. Central rod broken in middle ; indistinct in anterior portion, with no trace of lateral branches. *Antenna* of thirteen to twenty segments, usually sixteen segmented ; setae well-developed on basal segments, very small on distal ones. *Scuta* (Fig. 8 a–g) twenty-two in number including first which is reduced to a narrow oval plate with a pair of diagonal bands (Fig. 8 a). Triangular projections on posterior margins of scuta considerably longer than broad, and present only on scuta 2, 3, 4, 5, 7, 8, 9, 11, 12, 13, 15, 16, 19 ; distance between projections considerably more than their length from base to tip. Second scutum with distance from front margin to base of projection much less than length of projection. Setae on posterior scuta relatively long 0·013–0·016 mm. long. *Legs* (Fig. 8 i) short with very few setae. First leg fairly well-developed with anterior claw twice as long as posterior. Styli only represented by minute knobs. *Coxal plates* very small, coxal sacs only present at base of legs 3- 9. *Cerci* (Fig. 8 h) small, slightly more than three times as long as wide ; set with sparse, long setae ; terminal area long with seven transverse ridges on dorsal surface ; apical seta longer than terminal area, 0·026–0·032 mm. long.

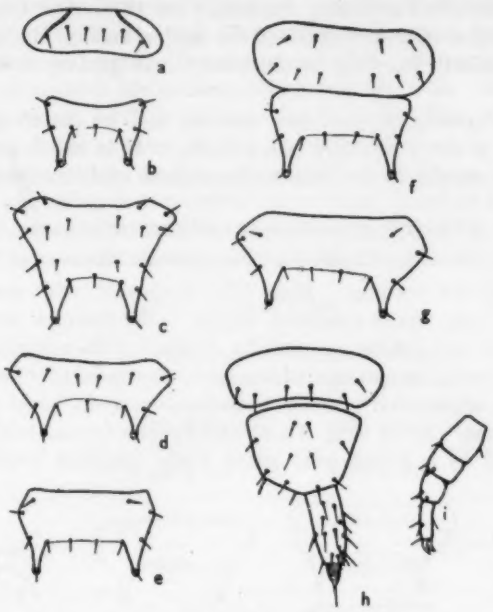

Fig. 8.—*Symphylellopsis subnuda* Hansen.
a–g, first to eighth dorsal scuta ; h, penultimate and last scuta and right cercus ; i, posterior view of last leg of left side. All ×180.

Chaetotaxy of scuta

No. of scutum	Greatest width of scutum (mm.)	Length of projection (base to tip) (mm.)	Distance between projections (mm.)
Second scutum	0·073–0·085	0·031–0·036	0·052–0·062
Third scutum	0·125–0·155	0·031–0·036	0·057–0·067
Fourth scutum	0·130–0·165	0·031–0·036	0·062–0·090
Fifth scutum	0·082–0·105	0·031–0·036	0·080–0·090

Type : In Copenhagen Museum. Type locality ; Palmi, Calabria. This description is based on specimens from Wimborne, Dorset, England.

Distribution : Previously recorded from Durham and Isle of Arran, Scotland. I have found specimens at Wimborne, Dorset; Redruth, Cornwall ; Isles of Scilly and in Bedfordshire. It is probably quite common but can be easily overlooked because of its minute size.

Comparative notes : There are only two other species of the genus described, and *S. subnuda* is most closely related to *S. arvernorum* Ribaut from which it is readily distinguished by the single scutum which corresponds with the third

pair of legs. Other distinguishing characters are the longer setae, particularly on the cerci ; greater distance apart of the projections on the scuta ; shape of the scuta, particularly the first and second ; and greater overlapping of the scuta.

Habits : This species is very slow moving and its distribution in the soil indicates that it is not a primary plant feeder. It is not found in such large numbers as some species of the genera *Symphylella* and *Scutigerella*.

SYMPHYLELLOPSIS ARVERNORUM Ribaut

1931 *Symphylellopsis arvernorum* Ribaut, Bull. Soc. Hist. nat. Toulouse **62**: 464.

Adult : Length 1·8–2·4 mm. *Head* (Fig. 9 w) oval, with sparse short setae 0·005–0·01 mm. long ; post-antennal organ with distinct tube opening to exterior. Central rod broken in middle, indistinct in anterior portion, with faint traces of lateral branches. *Antenna* of fourteen to nineteen segments, usually eighteen segmented ; setae well-developed on basal segments, very small on distal ones. *Scuta* (Fig. 9 a–t) twenty-one in number, including first, which is reduced to a broad oval plate with diagonal bands. Triangular

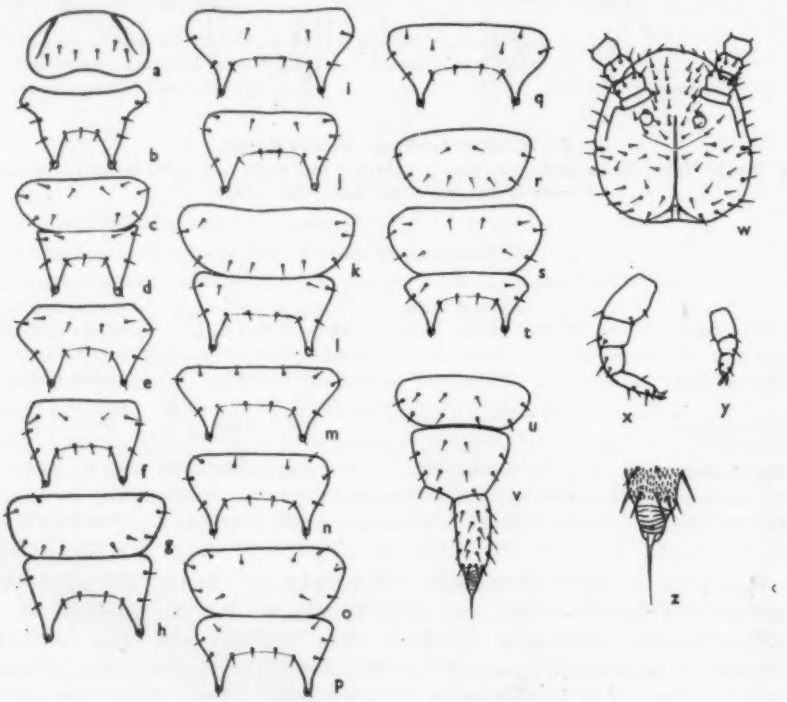

Fig. 9.—*Symphylellopsis arvernorum* Ribaut.
a–u, first to twenty-first dorsal scuta ; v, last scutum and right cercus ; w, dorsal view of head ; x, posterior view of last leg of left side ; y, posterior view of first leg of right side ; z, tip of cercus. All × 180 except z which is × 316.

projections longer than broad, present on posterior margins of scuta 2, 4, 5, 6, 8, 9, 10, 12, 13, 14, 16, 17, and 20 ; distance between projections only a little more than their length. Second scutum with distance from front edge to base of projection about the same as length of projection. Setae on posterior scuta relatively short, 0·010–0·013 mm. long. *Legs* (Fig. 9 x–y) short with very few setae. Anterior claw of first leg twice as long as posterior. Styli represented only by minute knobs. *Coxal plates* very small ; present at bases of legs 3–9. *Cerci* (Fig. 9 v–z) small about three times as long as wide ; set with sparse, short setae ; terminal area long with seven ridges on dorsal surface ; apical seta longer than terminal area 0·019–0·026 mm. long.

Chaetotaxy of scuta

No. of scutum	Greatest width of scutum (mm.)	Length of projection (base to tip) (mm.)	Distance between projections (mm.)
Second scutum	0·083–0·104	0·029–0·034	0·042–0·057
Third scutum	0·104–0·130	0·029–0·034	0·052–0·068
Fourth scutum	0·115–0·156	0·029–0·034	0·062–0·080
Fifth scutum	0·080–0·104	0·029–0·034	0·073–0·090

Type : in the collection of M. Ribaut. This description is based on a specimen from Axbridge, Somerset. Type locality : Orcines, France.

Distribution : Originally described from Orcines, and not previously recorded from Great Britain. I have found specimens at Cheddar and Axbridge in Somerset, and Warminster in Wiltshire.

Comparative notes : *S. arvernorum* is most closely related to *S. subnuda* Hansen and can be distinguished as shown under the heading of that species.

Habits : These are similar to those of *Symphylellopsis subnuda*.

Genus *SCOLOPENDRELLA* Gervais

1840 *Scolopendrella* Gervais, Rev. Zool. **2**: 279.

Head oval, slightly longer than broad, central rod broken in middle, distinct in both anterior and posterior portions, dividing anteriorly into two indistinct branches ending near base of antennae. Post-antennal organ small. Dorsal surface of head set with numerous moderately long setae. *Antennae* with fifteen to twenty segments bearing moderately long setae, secondary whorls of setae only weakly developed. *Scuta* seventeen in number ; first scutum vestigial, represented only by row of setae ; thirteen other scuta bearing paired triangular processes on posterior margins; all scuta except last two separated by intertergal areas, only last two divided by a simple suture ; posterior margins of scuta clearly-demarcated and bearing a transverse belt of longitudinal striae between the projections ; lateral margins of scuta curved and bearing another long seta in addition to the antero-lateral seta. *Legs* short, robust and sparsely setose ; claws almost equal in length ; first pair of legs well-developed, three segmented, almost half as long as last pair, with

posterior claw shorter and more curved than anterior. Styli rudimentary. *Coxal plates* with fully developed sacs at only bases of legs 3–9. *Cerci* short, sharply pointed, nearly conical, sparsely setose ; terminal area conical and not expanded, with intricate pattern of striae, apical seta about as long as terminal area.

SCOLOPENDRELLA NOTACANTHA Gervais

1840 *Scolopendrella notacantha* Gervais, Rev. Zool. **2**: 281.

Adult : Length 3·0–3·5 mm. *Head* (Fig. 10 p) oval, sparsely setose ; central rod broken in middle with short lateral branches, diagonal frontal branches indistinct. Post-antennal organ small. *Antenna* of fourteen to eighteen segments, usually eighteen segmented ; antennal setae simple, secondary whorl of setae not strongly developed and only present on distal segments. *Scuta* (Fig. 10a–g) seventeen in number, first vestigial ; posterior margins between projections semi-circular and bearing belts of longitudinal striae ; lateral margins of scuta curved and bearing another long seta in

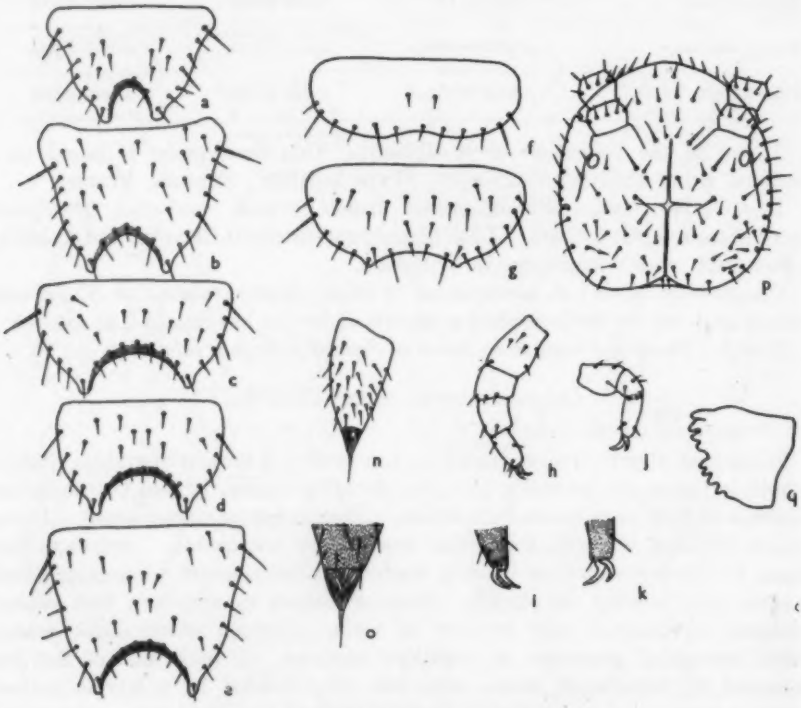

Fig. 10.—*Scolopendrella notacantha* Gervais.

a–e, second to sixth dorsal scuta ; f, g, fourteenth and fifteenth dorsal scuta ; h, posterior view of last leg of left side ; i, claws of last leg ; j, posterior view of first leg of right side ; k, claws of first leg ; n, dorsal view of right cercus ; o, tip of cercus ; p, dorsal view of head ; q, right mandible. All ×140 except i, k, o, q, which are ×316.

addition to the anterior-lateral seta. *Legs* (Fig. 10 h–k) short, robust and sparsely setose ; claws almost equal in length ; first pair of legs well-developed, almost half as long as last pair, with posterior claw shorter and more curved than anterior. Styli only rudimentary. *Coxal plates* fully developed as sacs only at bases of legs 3–9. *Cerci* (Fig. 10 n–o) short, nearly conical ; set with few setae ; terminal area conical, with intricate pattern of striae ; apical seta long, about as long as terminal area.

Chaetotaxy

No. of scutum	Length of antero-lateral seta (mm.)	Length of long seta in middle of scutum (mm.)	Length of typical marginal seta (mm.)
Second scutum	0·049–0·055	0·036–0·042	0·020–0·025
Third scutum	0·049–0·055	0·036–0·042	0·020–0·025
Fourth scutum	0·049–0·055	0·032–0·036	0·020–0·025
Fifth scutum	0·026–0·031	0·021–0·026	0·020–0·025
Sixth scutum	0·051–0·057	0·036–0·042	0·020–0·025

Type : In Copenhagen Museum. Type locality : Rome, Italy. Present description based on specimens from Torquay, Devon.

Distribution : Previously recorded from Durham. I have only found it at Torquay in Devon.

Comparative notes : *S. notacantha* is the only species of the genus so far described, so there is no difficulty in distinguishing it from *Symphylella* species to which it is most closely related. It can be distinguished by the well-developed first pair of legs and the striate belts at the posterior margins of the scuta.

Habits : It is one of the more slowly moving species, inhabiting similar situations to *Symphylella* species.

Genus *SYMPHYLELLA* Silvestri

1902 *Symphylella* Silvestri, *in* Berlese, *Acari Myriapoda et Scorpiones hucusque in Italia Reperta* **96**: 10.

Head oval, longer than broad ; central rod broken and distinct in both anterior and posterior portions, no lateral branches at break, diagonal frontal branches distinct. Post-antennal organ distinct, opening to exterior by numerous small pores. *Antennae* with fourteen to twenty-two segments bearing moderately long setae, secondary whorls only moderately developed. *Scuta* seventeen in number, first scutum vestigial, represented only by a line of setae ; thirteen other scuta bearing triangular processes on posterior margins, with no belts of longitudinal striae, lateral margins of scuta only slightly curved or straight. *Legs* fairly well-developed, bearing some long setae, claws nearly equal in length ; first pair of legs only represented by small protuberances behind head. Styli rudimentary. *Coxal plates* with

sacs only fully developed on legs 3–9. Cerci relatively long, with sides parallel for considerable part of length ; setae quite long ; terminal area bulbous and with transverse stripes, ending in a single long seta.

Taxonomic features

This is a difficult genus due to the variability in chaetotaxy. The chaetotaxy of the dorsal scuta is frequently asymmetrical with several more setae on one side than the other, and to some extent the shape of the scuta may be variable. This has led to a great deal of confusion and erection of a large number of species many of which may be invalid. Of the species described by Bagnall (1913) *Symphylella dunelmensis* is probably a synonym of *S. isabellae* Grassi and the three species *Symphylella horrida*, *S. delicatula* and *S. minutissima*, are as far as can be ascertained from specimens deposited in the British Museum (Natural History), synonyms of *Symphylella vulgaris* Silvestri. In the material available in the present study three well-defined species stand out, and these have been described with tables giving variation in chaetotaxy. A considerable number of specimens which will not fit into these species have been found, and it is hoped in the future to describe further species in this genus, with complete keys to the genus.

KEY TO BRITISH SPECIES OF *SYMPHYLELLA*

1. First scutum represented by a row of eight to twelve setae ; last pair of legs with four outstanding setae on outer dorsal surface of tarsus, posterior processes of scuta broad ..... *S. isabellae* Grassi
–. First scutum represented by a row of six setae ; last pair of legs with less than four outstanding setae on outer dorsal surface of tarsus, posterior processes of scuta narrow ..... 2.
2. No setae on inner edge of posterior processes of scuta ; last pair of legs with only two outstanding setae on outer dorsal surface of tarsus ; cerci short, with long setae, including two very long outstanding setae on outer margin of cercus ..... *S. hintoni*, sp. n.
–. At least one seta on inner edge of posterior processes of scuta ; last pair of legs with three outstanding setae on outer dorsal surface of tarsus ; cerci long, with short setae ..... *S. vulgaris* Hansen.

SYMPHYLELLA HINTONI sp. n.

Adult : Length 1·6–2·7 mm. *Head* (Fig. 11 i) longer than broad, with short setae 0·008–0·016 mm. long ; central rod distinct throughout length, only very slightly interrupted in middle ; without lateral branches ; indistinct diagonal branches from posterior end of central rod to base of antennae ; central rod without posterior projection. Post-antennal organ small and oval. *Antenna* of fifteen to nineteen segments usually eighteen segmented. *Scuta* (Figs. 11 a–g) with few setae ; first scutum only represented by row of six setae ; margins of scuta straight with sharp angles ; posterior processes narrow without obvious knob at tip. *Legs* (Fig. 11 l) short, with few long outstanding setae ; tarsus only about two and a half times as long as wide. Styli reduced to small protuberances. *Coxal sacs* fully developed at base of legs 3–9 only. *Cerci* (Fig. 9 h–k) small, short, conical; with long sparse setae, and with two oustanding setae on outer margin. Terminal area expanded and bearing seven or eight raised transverse striae ; single apical seta 0·026–0·024 mm. long.

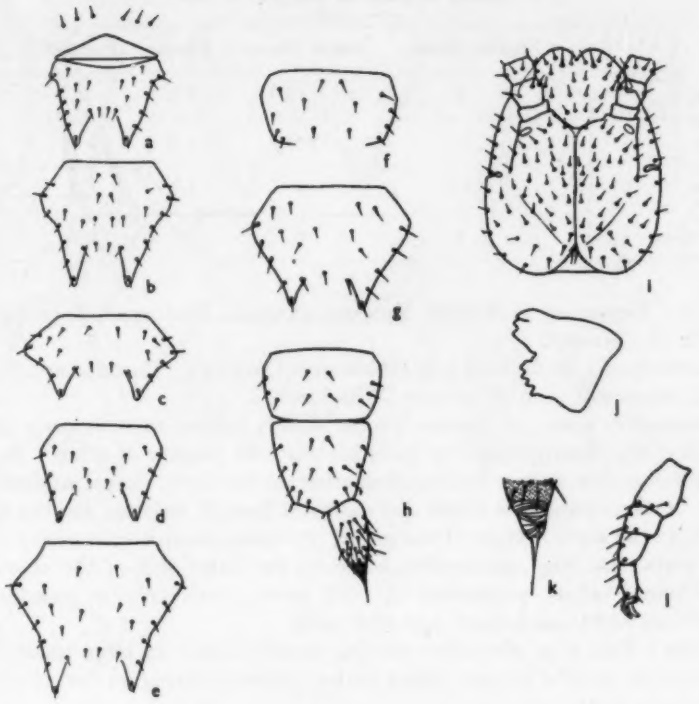

Fig. 11.—*Symphylella hintoni*, sp. n.

a–e, first to sixth dorsal scuta; f, g, fourteenth and fifteenth dorsal scuta; h, penultimate and last scutum and right cercus; i, dorsal view of head; j, right mandible; k, tip of cercus; l, posterior view of last leg of left side. All ×140 except j and k which are ×316.

Chaetotaxy

1. Dorsal scuta (based on twelve specimens from five localities).

No. of scutum	No. of setae between antero-lateral seta and apical seta	Length of antero-lateral seta (mm.)	Length of average seta (mm.)
Second scutum	2–4	0·013–0·016	0·008–0·10
Third scutum	3–5	0·013–0·016	0·008–0·012
Fourth scutum	2–3	0·013–0·016	0·008–0·012
Fifth scutum	2–3	0·013–0·016	0·008–0·012

2. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	2	1	1–2	2	6–7
Tibia	1–2	0–1	1–2	1–2	5–7
Femur	1–2	0	1–2	1–2	4–6
Trochanter	1	0	0	2–3	3–4

Type : Deposited in British Museum (Natural History). Type locality : Rosewarne, Cornwall.

Distribution : So far found at Rosewarne, Cornwall ; Cheddar and Fontnell Magna, Somerset ; and Westbury, Wiltshire*.

Comparative notes : *S. hintoni* is most closely related to *S. vulgaris* Hansen, but it is easily distinguished by its small size and paucity of setae. No other species has as few as two outstanding setae on the outer dorsal surface of the tarsus. Other characters which distinguish it from *S. vulgaris*, are the absence of setae on the inner surface of the scutal processes, sharp angles of the outlines of the scuta, two long outstanding setae on the outer side of the cerci, small post-antennal organ, possession of only seven teeth on the mandibles (*S. vulgaris* has eight), and short legs and cerci.

Habits : This is a very slow moving species found in large numbers. It does not seem to be a primary plant feeder, probably living on decaying matter and bacteria in the soil.

SYMPHYLELLA VULGARIS Hansen

1884 *Scolopendrella notacantha* Latzel, *Die Myriapoden der osterreichisch-ungarischen Monarchie* **2**: 11.

1903 *Scolopendrella vulgaris* Hansen, Quart. J. Micr. Sci. **47**: 1.

1913 *Symphylella vulgaris* Hansen, J. Linn. Soc. (Zool.) **32**: 195.

Adult : Length 2·4–3·5 mm. *Head* (Fig. 12 j) oval, with numerous short setae 0·008–0·029 mm. long ; mandibles with eight teeth ; central rod interrupted strongly in middle ; posterior and anterior branches distinct in entire length. Post-antennal organ circular, opening to exterior by pores. *Antenna* of fourteen to twenty-one segments, usually nineteen segmented ; secondary whorl of setae only weakly present on distal half of antenna. *Scuta* (Fig. 12 a–h) with processes longer than broad and with small knob at tip. *Legs* (Fig. 12 n–o) moderate in length ; sparsely covered with long setae ; anterior claw rather longer than posterior on last pair of legs. Tarsus four or five times as long as broad. Styli reduced to small protuberances. *Coxal sacs* fully developed at base of legs 3–9 only. *Cerci* (Fig. 12 k–l) about three times as long as broad, moderately setose. Terminal area expanded with eight or nine raised striae. Apical seta single 0·029–0·037 mm. long.

* I have also received specimens of this species from Dr H. Gisin, Geneva, Switzerland.

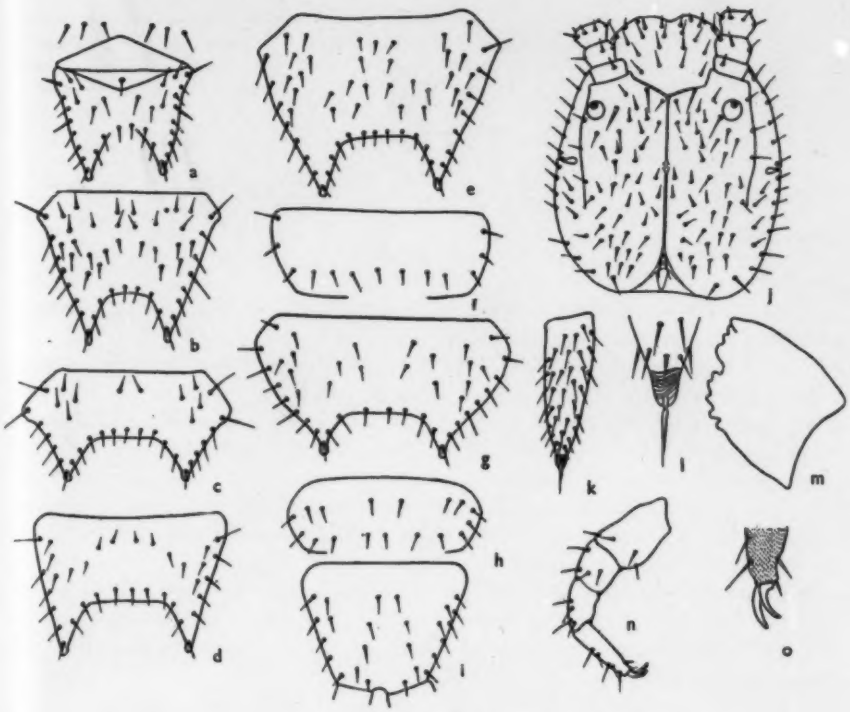

Fig. 12.—*Symphylella vulgaris* Hansen.

a–e, first to sixth dorsal scuta ; f, g, fourteenth and fifteenth dorsal scuta ; h, i, penultimate and last dorsal scuta ; j, dorsal view of head ; k, dorsal view of right cercus ; l, tip of cercus ; m, right mandible ; n, posterior view of last leg of left side ; o, claws of last leg of left side. All ×140 except l, m and o which are ×316.

Chaetotaxy

1. Dorsal scuta (based on seventy-one specimens from eighteen localities).

No. of scutum	No. of setæ between antero-lateral seta and apical seta	Length of antero-lateral seta (mm.)	Length of average seta (mm.)
Second scutum	4–7	0·034–0·042	0·013–0·023
Third scutum	5–8	0·034–0·042	0·013–0·023
Fourth scutum	4–6	0·034–0·042	0·013–0·023
Fifth scutum	4–6	0·029–0·034	0·013–0·023
Sixth scutum	6–8	0·031–0·036	0·013–0·023

2. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	3	1	1–3	3–5	8–10
Tibia	2	0	1–3	1–3	4–6
Femur	2	0	2–4	1–3	6–8
Trochanter	1	1	1–3	3–6	7–9

Type : In Copenhagen Museum. Type locality : Scilla, Italy. Present description based on specimens from Dawlish, Devon.

Distribution : Cosmopolitan. It has previously been recorded from numerous localities in the North of England, and it is very common in the South West of England. I have found it in thirty-two localities distributed in Gloucestershire, Somerset, Wiltshire, Dorset, Devon and Cornwall.*

Comparative notes : *S. vulgaris* is most closely related to *S. hintoni* and can be separated from this species as shown under the heading of the latter species. It is also closely related to *S. isabellae* Grassi, and it can be distinguished from this species by its much smaller size, presence of only three outstanding setae on the outer dorsal surface of the tarsus, much shorter cerci with fewer setae, narrower processes on the posterior margins of the scuta, only six setae representing the first scutum, and the presence of a projection at the posterior end of the central rod.

Habits : These appear to be similar to those of *S. hintoni*.

SYMPHYLELLA ISABELLAE Grassi

1886 *Scolopendrella isabellae* Grassi, *Mem. R. Accad. Sci. Torino* (2) **37**: 594.
1913 *Symphylella isabellae* Grassi, J. Linn. Soc. (Zool.) **32**: 195.

Adult : Length 2·3–4·6 mm. *Head* (Fig. 13 f) oval, with numerous setae 0·010 mm.–0·047 mm. long ; mandibles with seven teeth. Central rod interrupted strongly in middle ; posterior and anterior branches distinct in whole length. Post-antennal organs circular, opening to exterior by pores, not so distinct as *S. vulgaris*. *Antenna* of fifteen to twenty-two segments usually eighteen segmented ; secondary whorl, and traces of tertiary whorl of setae present on distal half of antenna. *Scuta* (Fig. 13a–e) with processes about as long as broad, with only slight traces of knob at tip. First scutum represented by eight to twelve setae. Scutal setae long. *Legs* (Fig. 13 h–i) long, sparsely covered with long setae ; anterior claw slightly longer than posterior on last pair of legs. Tarsus about five times as long as broad. Styli reduced to small protuberances. *Coxal sacs* fully developed at base of legs 3–9 only. *Cerci* (Fig. 13 j–k) four to five times as long as broad, densely covered with short setae. Terminal area expanded with eight to nine raised transverse striae ; apical seta single 0·028–0·039 mm. long.

*I also found this species commonly in Wisconsin, U.S.A.

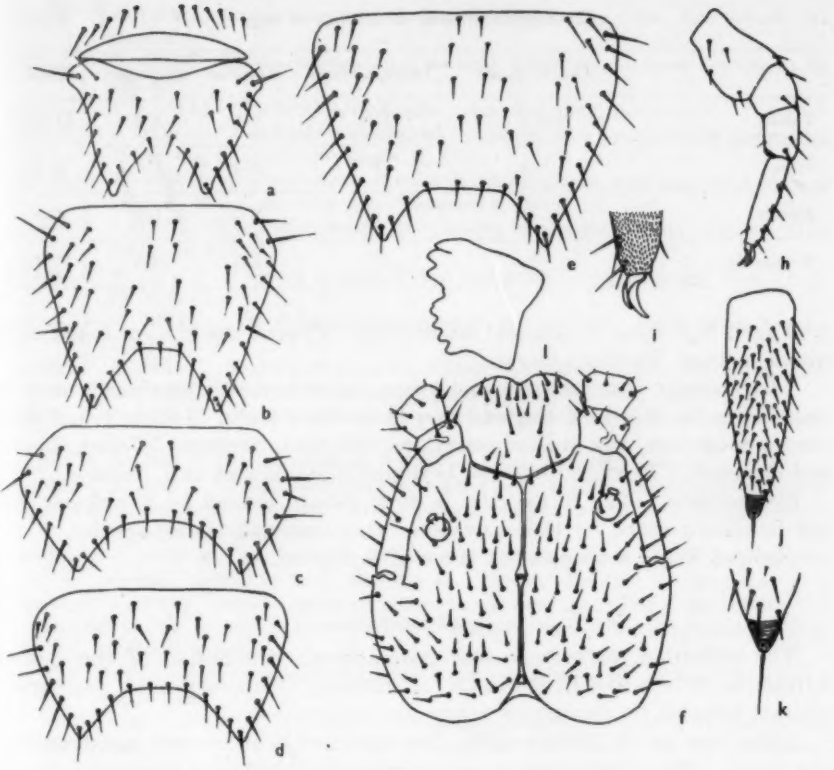

Fig. 13.—*Symphylella isabellae* Grassi.

a–e, first to sixth dorsal scuta ; f, dorsal view of head ; h, posterior view of last leg of right side; i, claws of last leg of left side ; j, dorsal view of right cercus ; k, tip of cercus ; l, right mandible. All ×140 except i, k and l which are ×316.

Chaetotaxy

1. Dorsal scuta (based on fifty-six specimens from twenty-four localities),

No. of scutum	No. of setae between antero-lateral seta and apical seta	Length of antero-lateral seta (mm.)	Length of average seta (mm.)
Second scutum	5–8	0·043–0·054	0·013–0·034
Third scutum	4–9	0·043–0·054	0·013–0·034
Fourth scutum	3–7	0·047–0·060	0·013–0·034
Fifth scutum	3–7	0·042–0·050	0·013–0·034
Sixth scutum	5–11	0·052–0·063	0·013–0·034

2. Number of setae on last pair of legs.

	Outer, dorsal	Inner, ventral	Anterior	Posterior	Total
Tarsus	4–5	1–2	4–6	3–6	14–18
Tibia	2–3	1	3–4	1–4	9–12
Femur	2	0	2–4	1–3	6–9
Trochanter	1	2–3	2–7	4–9	11–18

Type : Not given in original description. Present description based on a specimen from Dawlish, Devon.

Distribution : Not common in Europe ; only recorded previously once or twice from the North of England and twice from Italy. I have found it in twenty-seven localities in Gloucestershire, Wiltshire, Somerset, Dorset, Devon and Cornwall. It seems to be just as common in this area as *S. vulgaris*.

Comparative notes : *S. isabellae* is most closely related to *S. vulgaris* and can be distinguished by the characters listed under the latter species.

Habits : These are similar to those of *S. hintoni*.

SUMMARY

The collection, occurrence and geographical distribution of the British Symphyla is discussed. Methods of making temporary and permanent mounts suitable for taxonomic study are outlined.

Eight species of *Scutigerellidae*, belonging to three genera are described, one species being new to science and four new to the British Isles. Six species of *Scolopendrellidae* belonging to three genera, one species being new to science and one new to the British Isles are described.

Symphyla vary considerably in size and chaetotaxy and because of this as many specimens as possible from a wide range of localities have been studied ; in all, specimens from 317 localities. This has enabled the range of variation to be expected in each species to be outlined.

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Thanks are due to the numerous workers who kindly sent me specimens ; to Dr G. O. Evans, British Museum (Natural History) for placing material and facilities at my disposal, and to Dr H. E. Hinton, University of Bristol, for his encouragement and advice. I have pleasure in naming *Symphylella hintoni* after him.

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TALKING BIRDS AND THE MODE OF ACTION OF THE VOCAL APPARATUS OF BIRDS

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(With 6 figures in the text)

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INTRODUCTION

The essential problem with which the present paper is concerned is that of the mode of action of the bird vocal organs in producing sounds of very great diversity. On the one hand we have the very restricted vocabulary, comprising only a few notes, possessed by many of the "lower" families of birds such as the Colymbidae, Podicepidae, some of the Galliformes and some of the Laridae. On the other hand we come to the extreme development of bird vocalizations in groups such as the Turdidae (*sens. lat.*, including Turdinae, Thrushes and Nightingales; Sylvinae, Warblers and Miminae, Mocking Birds). Moreover there is the astonishing mimicry of the human voice which can be achieved by a well-trained parrot or Budgerigar (*Melopsittacus undulatus*) or by the best mimics amongst the Sturnidae (*Sturnus*, Starlings, *Eulabes*, Mynah).

The early bird anatomists, of course, noted the structure of the syrinx and its related elaborations of the trachea forming what appear to be complex resonating chambers. It is, however, far from clear how, even in the less highly evolved groups of birds, these supposed resonating chambers actually affect the voice production. As Pycraft (1910) points out, although the Cassowaries have perhaps the simplest form of syrinx, yet they can give vent to a considerable variety of sounds including a noise that has been described as a deep roar. The emus which are equipped with an elaborate inflatable sac associated with the trachea do not thereby seem able to produce greater variety or volume of sound. Again, among the ducks a great many remarkable modifications have been described but in no case does any clear correlation seem possible between the tracheal structure and the type or variety of sounds

produced. Moreover, as Pycraft points out, if some of these structures in ducks are for modifying the voice then it is curious, to say the least, that in many ducks the female, which has no resonator, has the louder voice and that ducks with precisely similar resonators have entirely different calls. To some extent passerine birds provide a similar puzzle, at least in so far as the possession of an elaborate syringeal organ does not necessarily imply elaborate vocalizations. Nevertheless, the groups, which contain the best songsters are certainly those in which the syrinx has the most complex musculature. Many of these complexities were described long ago in the writings of Owen (1860), Gadow (1891, 1896), Shufeldt (1890), Häcker (1900). After that date, apart from the excellent paper of Rüppell (1933), nothing of note seems to have appeared until the study of Miskimen (1951).

HUMAN VOCAL APPARATUS

Helmholtz (1821–1894) carried out his fundamental studies on the production of sounds very nearly a hundred years ago. His book on " Sensations of Tone " was published in 1862. This laid the foundations for the comprehension of the mode of action of the human vocal organs, but even though the study of human vocalization has been pursued fairly vigorously since that time, we have still a great deal to learn about our own methods of song and speech. It is, therefore, not surprising that our ignorance of the production of bird sounds is still immense. However, it now seems profitable to consider the bird vocal organs once again in the light of recent developments in our understanding of the human vocal apparatus.

In man there is, of course, a vibratory apparatus consisting of the vocal chords. Voiced sounds are thus modulated by the changing tensions exerted on the cords by the associated muscles as the air passes over them. Voice is further modulated by tongue and lips and, in properly controlled speech and song, by appropriate changes in the shape and dimensions of resonating chambers which, in our case, are the pharyngeal, oral and nasal cavities. Thus our vocal cords determine the pitch of the voiced note and the resonating system is made to conform. This, Mackworth-Young (1953) points out, is due on the one hand to the vigorous and precise action of the vocal cords, and on the other to the fact that the throat cavity in which they are placed is easily variable in shape and has elastic yielding walls. He adds : " If our throats were plain tubes of metal or hard wood their resonating tones would be so rigid and strongly defined that the vocal cords would be unable to maintain any other frequencies against them. As things are, the resonances of the throat cavity, though adequate for reinforcing the vocal note, are not sufficiently strong or inflexible to oust the cords from their control of the pitch. Accordingly, the throat cavity and, with it, the mouth cavity also are content to let the vocal cords dictate the prime tone and to modulate their own resonances so as to reinforce such partials of the tone as lie within their respective compasses. The modulation is effected by movements, principally, of the tongue, lips and jaw which alter the size and shape of the cavities or of their openings, or both, and thus produce resonances of different pitch." When we compare wind instruments with the human voice we see that most of them are

equipped with finger holes, stops, valves or other devices by which the resonating length of the tube can be changed and different fundamental tones thus achieved. The sounds produced by the passage of air through the instrument will, therefore, in the first place be due to the restriction imposed by the rigid walls of the musical instrument. In those instruments where there is a vibrator in the form of a reed this is, of course, passive, and the unyielding action of the resonating chamber forces the reed (or, in the case of the trumpet, the vibrating lips of the player) to conform. The tonal quality of these two is similarly due primarily to the particular series of partials or harmonics which the resonators reinforce—in other words, to the spectrum of frequency components.

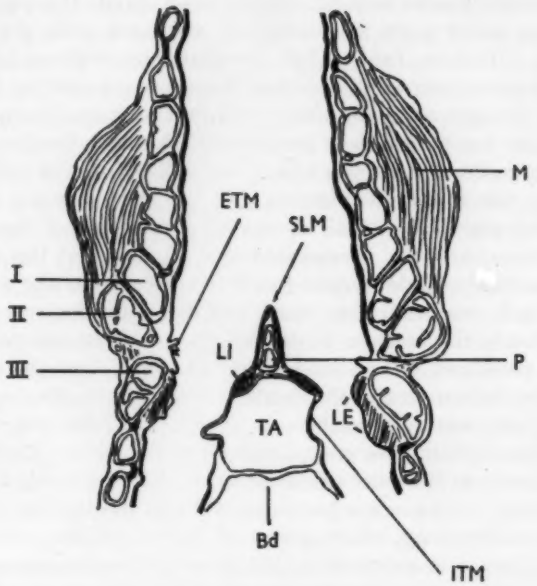

Fig. 1.—Longitudinal section through the syrinx of a male Blackbird to illustrate the typical structure (modified from Häcker). Bd=Bronchiodesmus membrane. ETM, ITM=Exterior and interior tympanic membranes. LE & LI=External and internal lips. M=Tracheo-bronchialis muscles. P=Pessulus. SLM=Semi-lunar membrane. TA=Extension of anterior thoracic air sac. I, II and III Bronchial semi-rings.

AVIAN VOCAL APPARATUS

The question then arises : how far is the avian vocal apparatus like such wind instruments ? A section through a characteristic bird syrinx, whether it is quite unspecialized as in the domestic fowl or highly efficient for song as in the Blackbird (*Turdus merula*), reveals a structure which is astonishingly uniform (Fig. 1). There is a semi-lunar membrane attached to a bony rod, the pessulus, stretched across the chamber at the point where the two bronchi unite. This membrane, while it must obviously be set in motion by the passage

of air, does not appear to have, in most birds, the direct muscular attachments which would be necessary if it was to act as a vibrator in the same masterful manner as do human vocal cords. Besides this membrane there are, however, two other pairs of membranes, the internal and external tympaniform membranes. These may not only have muscles attached to them but are also situated so that muscles which control the movements of the adjacent tracheal semi-rings will be effective in controlling the tensions in them. While the essential structure of this organ seems to be astonishingly uniform throughout, we do, however, find big differences in the development and situation of the syringeal muscles. In the domestic fowl Tymms (1913) showed that the syringeal muscles have no very close relation to the tympanic membranes. In the Blackbird (*Turdus merula*), on the other hand, Häcker (1900) showed that there are seven pairs of muscles as compared with the single pair in most Gallinae. (Gadow, 1896, points out that some Gallinae have no muscles in the trachea and syrinx at all, but that this is not a primitive feature but one that has been brought about by loss). In a gull such as a Herring Gull (*Larus argentatus*) there are two pairs of muscles, the broncho-tracheales and sterno-tracheales only. The former pair will, in the gulls, thus give a slight possibility of controlling the tympanic membranes. In the domestic fowl, however, there seems no possibility at all of any direct control of these membranes. These facts seem to imply inescapably that in many of the more primitive birds with the less well developed tracheal musculature the vocal apparatus must be acting in essentially the same way as a wind instrument and that it must be primarily the trachea which determines by its resonance the nature of the sound produced. Such modulation as can be brought about is in this case the result of the action of the broncho-trachealis in affecting the form and dimensions of the resonating tube. It would seem that the vibrating membranes must be entirely passive and subservient to this. That this is indeed the general picture in the more primitive birds seems to be implied by the work of Rüppell (1933). He made a particular study of the Herring Gull, comparing with it, as to morphology, other species of *Larus* and the genera *Grus*, *Anser*, *Gallus* and *Cygnus*. It seems then that there are sound reasons for making a functional comparison between the vocal structures of some birds and some types of wind instrument. However, even here the position is not entirely clear because, although most birds with powers of elaborate vocal production do possess a complex equipment of syringeal muscles, there are exceptions—for instance, the Wood Pewee (*Myochanes virens*) has a beautiful and complex song (Craig, 1943) although, according to Miskimen (1951), it has only three pairs of syringeal muscles as against seven pairs in a number of other forms.

A FUNCTIONAL COMPARISON BETWEEN THE AVIAN AND HUMAN VOCAL APPARATUS

Having given one part of the story, let us look at the matter from another angle and see what understanding can be reached by comparing the action of the vocal apparatus in bird and man. Miskimen (1951) is the only author who has attempted an experimental and functional analysis of the mode of action of the vocal apparatus of song birds. In mammals, of course, the voice is produced during exhalation, which is the passive phase of respiration, and it had been

assumed that the vibrations of the semi-lunar membrane were the prime cause of vocalization and that the sound must be produced while the air is entering the bird's lungs—the passive phase in bird respiration thus corresponding vocally to our exhalation. J. Arthur Thomson (1923), however, as well as some other writers, assumed from various pieces of circumstantial evidence that the voice in birds must be produced during the active phase of respiration, that is while the muscles of the thorax are forcing air from the lungs. Miskimen set out to test this by applying a syringe to the severed end of the trachea of an anaesthetized Sparrow (*Passer domesticus*) and forcing air through the respiratory tubes in alternating directions by compressing and releasing the bulb. No sound was produced by forcing air into the trachea, but when the bulb was released and the air drawn back into it, the bronchial tubes collapsed and a chirping noise was made. The internal tympaniform membranes just above the insertion of the bronchiodesmus membranes on the first bronchial half-rings were seen to vibrate freely and rapidly in the inter-bronchial space. The next experiment was to force air out through the syrinx by pressure from within. When air was forced into the air sac and drawn out through the trachea a sound was produced like that when air was drawn out from the tracheal end. A considerable pressure had to be applied before a sudden loud chirp was heard. In the Starling (*Sturnus vulgaris*) the trachea was cut off close to the syrinx and the semi-lunar membrane entirely removed. Air was then passed through the syrinx as before and sounds were produced unchanged without any apparent modification of tonal quality. From these experiments it was concluded that in the song birds sound is produced during the active or exhalant phase of respiration, that the semi-lunar membrane has no important function, if any, in the production of sound and that the sound originates in the vibrations set up in the tympaniform membranes by the passage over them of air from the lungs. These three conclusions seem to be as well established as any that we at present have. However, it may be doubted whether the conclusion that the semi-lunar membrane is functionless is, in fact, very convincing ; nor does there seem to be any sound basis for the assumption of some earlier workers that if the semi-lunar membrane is to be activated it must be by an inward passage of air. Nevertheless, the picture provided by the work of Miskimen on the sound production of passerine birds gives an impression of something very much more similar to the human voice than that which emerges from the work of Rüppell. We have here at least two pairs of membranes, the tension of which can quite clearly be modified by special groups of muscles and we have also ample equipment for modifying the shape, resistance and dimensions of the trachea or wind-pipe, so there is at least one resonator which can be actively modulated to conform with the vibrations of the tympanic membranes.

The recent advance which has made the subject worthy of renewed discussion is the development of the sound spectrograph. This instrument is now so well known amongst workers on acoustic phonetics and among zoologists concerned with the production of sounds that a description is unnecessary. An account from the point of view of the student of bird song will be found in the paper by Thorpe (1958) and more detailed descriptions can be sought in

the books by Potter, Kopp & Green (1947) and Joos (1948). Suffice it to say here that the apparatus translates a complex sound into a visual pattern and analyses it in terms of frequency (vertical scale) against time (horizontal scale). One of the striking features which has emerged from the study of bird vocalizations is the evidence that there is in some birds a double or multiple sound-producing mechanism. Thus Potter, Kopp & Green reproduce a sound spectrograph of the song of a Brown Thrasher (*Toxostoma rufum*) in which, at certain points in the song it is quite clear that two notes, harmonically

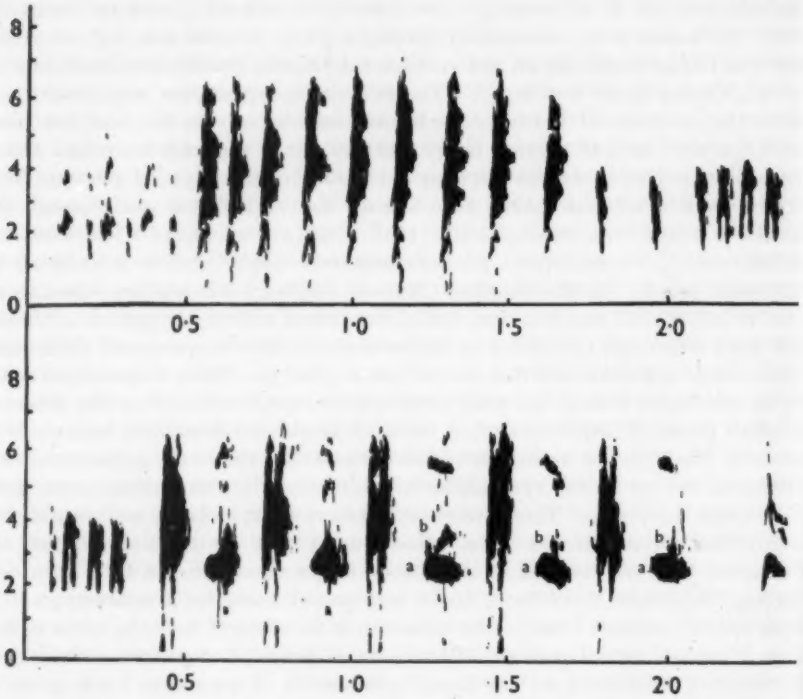

Fig. 2.—"High front" sounds of very short duration and great frequency range alternating with notes of two harmonically unrelated fundamentals (a) and (b) sounded simultaneously as produced by the Reed Warbler (*Acrocephalus scirpaceus*). Vertical scale: frequency in kilocycles per second. Horizontal scale: time in seconds.

entirely unrelated, are being sounded at the same time. I have analysed the song of the Reed Warbler (*Acrocephalus scirpaceus*) (Fig. 2) which shows a similar effect, and Borrer & Reese (1956) have shown that with the Wood Thrush (*Hylocichla mustelina*), one of most beautiful songsters, there is some overlapping of notes with one note beginning before the preceding note ends, thus resulting in the bird uttering more than one note at a time. In one song which they have recorded there is a moment of about 0·1 seconds in length when four separate notes are uttered simultaneously. It thus appears that

there must be, in some birds at least, more than one vibrator at work and if the record of Borrer & Reese is substantiated, there may be as many as four. As we have seen above, these could be the two sets of tympaniform membranes and thirdly perhaps the semi-lunar membrane. The fourth membrane is yet more questionable. Shufeldt (1890) described in the Raven (*Corvus corax*) two pairs of muscles which can affect the structure in the superior larynx known as the *rima glottidis*. One pair of muscles (*constrictor glottidis*) when firmly contracted efficiently close the *rima*. This pair has as antagonist the *thyreo-arytenoideus* which, by pulling the arytenoid bones outwards, will tend to open the *rima*. Owen in 1866 had assumed from the simplicity of the structures in this region and from the relation of the superior larynx to the gape of the bill, that the *rima* could not be considered as influencing the voice " otherwise than by ' dividing ' or articulating the notes after they are formed by the lower larynx " (syrinx). That the superior larynx does function as Owen suggested, as a start-stop modulator for the voice, and that the voice is produced by the syrinx seems undoubted. Whether he was correct in assuming that the larynx can do nothing else appears, in the light of recent studies, much more questionable. Arthur Thomson (1923, p. 125) obviously considers that membranes on either side of the glottis can, in some species, be functioning as vibrators. There is, then, no insuperable difficulty in seeing how the multiple notes of some song birds might be produced. When, however, we come to consider the imitative abilities of birds such as parrots, starlings and mynahs, the problems seem far harder to resolve.

When we look at the sound spectrograms of the human voice we can gather a great deal of information as to the way in which the sounds that make up human speech are produced. First, of course, there are the consonantal stopped sounds such as " p ", " b", " t ", " d ", " k " and " g " which merely involve, as students of phonetics have long recognised, different ways of stopping and starting sounds more or less suddenly, with more or less explosive force and with greater or less infusion of higher frequencies. These different consonants are, of course, produced by the use of different parts of the mouth—lips, tongue, and palate and combinations of these. So we would expect birds, when they stop and start their sounds (which they can do with extreme suddenness) to produce *something* like our consonants, but since the bird's tongue, larynx and mouth cavity are so different from ours, we should not expect the sound spectrograms of bird voices to show more than a very slight and general resemblance between bird consonants and our own, and this conclusion is, in fact, borne out by experiments. When we interpret bird sounds in human words we have, of course, no choice but to include the characteristic consonants and vowels which make up those words ; but the consonants we include may have little or nothing corresponding to them in the actual voice of the bird. The voice of the Wood Pigeon (*Columba palumbus*) may remind us of the phrase " Take two cows, Taffy " but it could equally well be "Tape goo gows, daddy" and indeed we could leave out the consonants altogether without much loss. Similarly, we think *Cuculus canorus* says " Cuckoo", but are we sure it does not say " Guggoo " or even " Puppoo "? The sound spectrogram gives no reason for thinking that one simile is much better than

another. In fact, consonants in bird voices are not generally recognisable except the fricatives "f", "v", "θ", "s", "z", "3", "x" and "ch" which are, on the whole, of relatively high frequency. The distinguishable series of stops which have already been mentioned are very little in evidence and do not appear to have anything like the vocal quality of our own, but a glance at the sound spectrographs of some bird vocalizations is sufficient to show that extreme "high front" sounds are common. These are sounds containing a big range of frequencies such as we normally associate with fricatives coupled with an extremely efficient mechanism for start-stop modulation. If these "high front" sounds are of very short duration, i.e. 1 to 20 milliseconds, they are heard as clicks without any definite pitch (Fig. 2). Sounds of big frequency range and very steep slope of onset are perhaps the most characteristic feature of bird songs (Fig. 3). There seems little doubt that

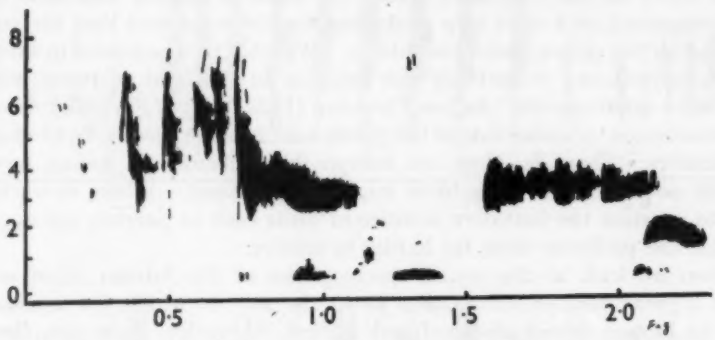

Fig. 3.—Typical bird song notes with a great frequency range and very steep slope of onset, as illustrated by the Robin (*Erithacus rubecula*).

the exact manner of onset, represented by the initial slope of the mark on the sound spectrogram, does have a big influence in conferring distinctive tonal quality, at any rate as perceived by our ears, to sounds which are in themselves —as is clear from the sound spectrograph—largely devoid of those harmonic partials on which the tonal quality of the sounds produced by musical instruments depends. Any similarities there may be with human consonants, therefore, depend on the range and relative intensities of the higher frequencies present. In human speech consonants are, in fact, complicated according to which vowels precede or follow them and whether these are "voiced" (modulated by the activities of the vocal cords) or "unvoiced", but these are matters which do not at present concern us.

The question of the bird production of vowels is, however, of particular significance. Phoneticians recognise twenty-three different vowel or vowel-like sounds in human speech. The vowels are, broadly speaking, the incidental result of the fact that we human beings have more than one main resonator. As Mackworth-Young points out, the vowels occur whenever the throat or mouth cavities are stirred into resonance simultaneously, whether the stimulus is due to vocal cords, as in speech and song (when the sound is said to be voiced or whether it is merely due to an airstream passing through both

cavities, as in whispering. "The only necessary condition is that the mouth should be open. We cannot speak, sing, whisper or even pant, without uttering a vowel*". There are four types of modulation which occur in speech: (1) start-stop, (2) vocal cord, (3) frictional, and (4) cavity modulation. Nos. (1) and (3) affect the flow of air from the lungs. Nos. (2) and (3) convert the flow into audible sound waves and (4) broadly speaking, varies the quality of the sound. The different types of consonants are produced by different combinations of these types of modulation but always containing (1) or (3) or both. When pure vowel and vowel-like sounds are produced in ordinary speech only (2) and (4) occur. In producing vowels the coupled cavities of mouth, nose and throat act in co-ordination on the overtones produced by the vocal cords (and to some extent by frictional modulation) and, by suppressing some, give an apparent reinforcement that we recognise as the vocal resonance. These vocal resonances in the vowels are determined by the shapes and sizes of the resonators and are under very precise control by the movements of the lips, jaw, tongue and soft palate; but it stands to reason that this cavity modulation will affect the sounds produced by the vocal cords very much more than those produced by frictional modulation since the sounds produced by the vocal cords are behind the cavities concerned, whereas those produced frictionally are in front.

The characteristics of vowels as an expression of the resonances of these three main cavities are well illustrated by sound spectrograms. Fig. 4 shows the kind of patterns produced when the six main vowels are sounded. It will be seen that there are characteristic resonance bars which correspond to the frequencies at which the vocal resonances occur. There are actually four of these, numbered from below up, but the fourth may be very faint or imperceptible. The patterns of the vowels and vowel-like sounds are characterized by different combinations of bars. Of the resonance bars most frequently present in the vowel patterns, the second bar is the most important one and this is known as the "hub". Bar one, the lowest, is limited in movement to a small interval at the bottom of the pattern, while bar three is both limited in its movement and is often weak and sometimes absent. Bar two, however, derives its significance from its relationship with one and three. The hub is thus the position of bar two, and can be defined as "the visible or hidden position of bar two when the vowel is sounded alone" (Potter, Kopp & Green).

* The throat resonance in human singers appears to be governed entirely by the vocal note regardless of which vowel is being produced. When however we neither sing nor speak but only whisper, the vocal cords do not meet so there is no vocal note at all. We are therefore unable to control the pitch. When we whisper a vowel all we do is to put our mouth cavities in a proper position for producing that vowel and allow air to pass through them, thus exciting the resonance of the cavities. As is well known to experienced singers, under such circumstances the pitch of a given vowel is constant for a given person in normal health, assuming that his or her cavities are not blocked as a result of a cold or other disease. This is of great value to singers because it means that a whispered vowel is always of the same pitch, this being determined by the characteristics of the cavities concerned in the particular individual. Thus a singer who lacks the good fortune to be the possessor of absolute pitch can achieve a very creditable substitute by whispering to himself a particular vowel, it may be "o" or "e", knowing from past experience that this will always give him a certain invariable pitch reference. (I am indebted to Professor G. C. Varley for drawing my attention to this matter.)

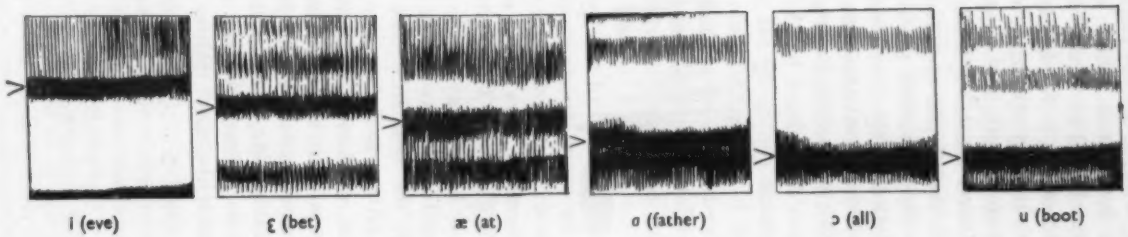

Fig. 4.—Patterns of resonances of the three main cavities produced when the six main vowels (i, e, æ, œ, o and u) are sounded. The hub of the vowel (formant 2) is indicated in each case.

Similarly, as we have said, consonants have potential vocal resonances which may or may not produce visible bars in their pattern. (They are much less in evidence in sound spectrograms because, as we have seen, the modulators producing the consonants are in front of the resonating cavities; but a human consonant may have a hub which is defined in just the same way—as the hidden position of bar two). When we compare the six vowels, each of which has a different hub, we can see why—since the vertical scale is one of frequency—a succession of vowels can give us an impression of a series of sounds changing pitch. This brings us back, then, to the question: what, if anything, in the way of vowels can a talking bird produce? At first sight, the vocal equipment does not appear to have the cavities necessary to enable the bird to produce anything at all similar to our vowels. True, we often think and speak as if we believe birds to be uttering vowels. We might add the Curlew (*Numenius arquata*) to the Pigeon and Cuckoo already mentioned, and there is a common impression that the Yellow Hammer or Yellow Bunting (*Emberiza citrinella*) says "I want a little bit of bread and no cheese". We hardly need the sound spectrograph to tell us that the Yellow Bunting really says nothing of the kind. Why is it, then, that such little phrases serve to remind us of particular bird songs? It is chiefly because the rhythm is appropriate and because the vowels that we include in such phrases reflect approximately the same changes in fundamental pitch that are found in the bird song. But although there are many early records alleging that Robins and other song birds can learn to talk (Lack 1943), none of the sound spectrograms of any of the ordinary song birds that I had hitherto myself investigated or seen described had given any indication that birds can produce anything approximating to a human vowel.

This conclusion raised immediately the problem of talking birds. Surely parrots and budgerigars at least produce something like our vowels? However, such records as I was able to examine gave little support to any such conclusion and for a long time I was inclined to believe that when a bird imitated the vowels of human speech, all it did was to produce the right pitch changes, so giving the impression that a good imitation of human words had been effected. Recently, however, I have had to revise this opinion as a result of hearing and having access to recordings of an Indian Hill Mynah (*Eulabes religiosa*) in the possession of Mr and Mrs R. B. Klopman; to whom I am very much indebted for co-operation and for making available good recordings of this delightful bird. It will be seen at once from the sound spectrograms shown in Figs. 5 and 6 that whatever may be lacking in the vocalization of other talking birds, this one successfully produces at least four perfectly genuine vowels, and can probably accomplish many more. The sound spectrograms speak for themselves, but it will be seen that there is perfectly clear evidence of three and sometimes four vocal resonances and that some at least of these (Nos. 2 and 3) are under precise control.

It is clear from this result that the acoustic study of bird sounds has now far outdistanced the studies of the morphologist and that a most attractive field of investigation for the avian anatomist has been re-opened. At present we can do no more than speculate as to the resonating cavities which must be involved in the production of vocal mimicry of the order shown by *Eulabes religiosa*.

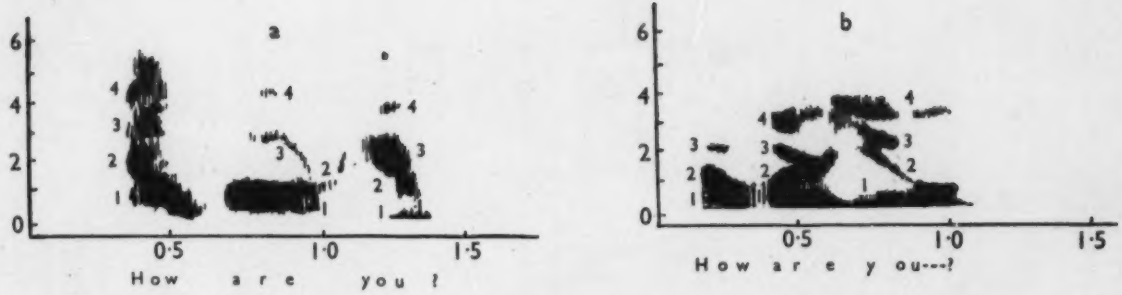

Fig. 5.—The phrase "How are you ?" spoken by : (a) Indian Hill Mynah ; (b) Adult human male, New Jersey accent. Vowel formants are numbered 1–4. N.B. To facilitate comparison the human speakers, when enunciating the phrases from which Figs. 5b and 6b & c were made, deliberately modelled the accent and intonation of their words on those of the bird. This however did not affect the vowel structure which is typical of human speech.

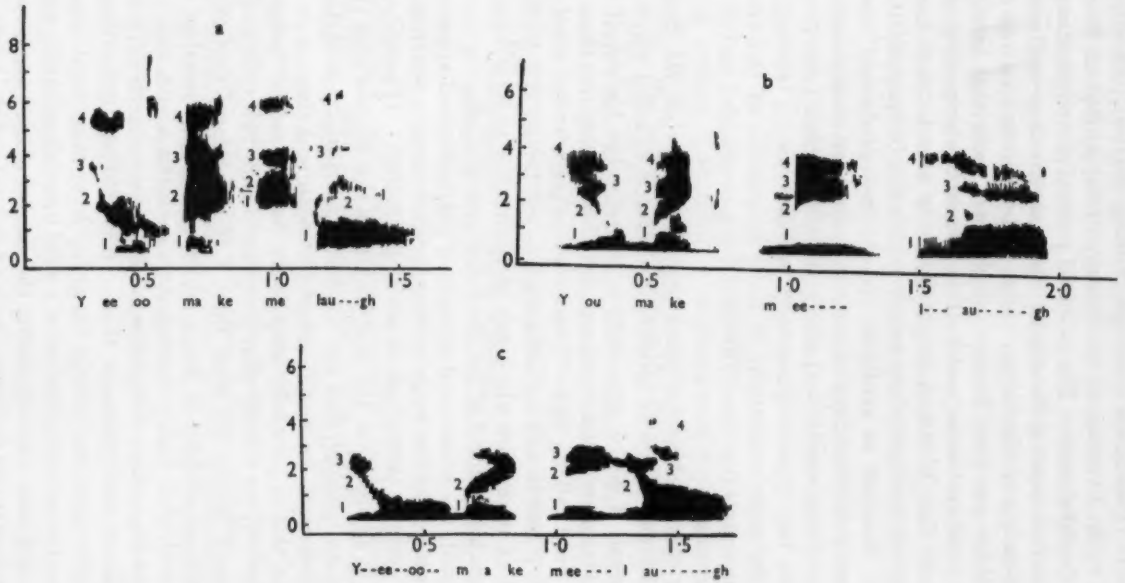

Fig. 6.—The phrase " You make me laugh " spoken by : (a) Indian Hill Mynah ; (b) Adult human male, New Jersey accent ; (c) Adult human female, New England accent.

Recently, through the kindness of the staff of the Phonetics Department of the University of Edinburgh, I was enabled to see and hear the apparatus known as P.A.T. (Parametric Artificial Talking Device). This instrument was developed by W. Lawrence at the Ministry of Supply Signals Research and Development Establishment. The essential parts of the apparatus (W. Lawrence, 1955, and Ladefoged & Broadbent, 1957) are first a generator producing a pulse corresponding to the larynx pulse, which serves to excite the vocal tract. Then there are four formant generators, resonating circuits which respond to the pulse excitation, and finally a generator which will produce noise corresponding to that produced in the fricative sounds of human speech. This apparatus will synthesize any speech which can be specified in terms of six variables. Samples of synthetic speech thus produced "nevertheless sound so natural that recordings of some sentences are always confused with recordings of normal speech" (Ladefoged & Broadbent, 1957). The six variables which the apparatus normally specifies are (1) intensity, and (2) frequency of the pulse excitation, (3 to 5) frequencies of the lowest three formants of the vowels (the fourth formant being invariable), and (6) intensity of the fricative noise.

On hearing this machine the point immediately struck me that whereas with all six variables normally specified, the speech sounded almost (though not quite) normal, if No. 5 was omitted (namely, the highest of the three variable formants) some of the words sounded uncommonly like those produced by a not very good talking bird. This seems to point to the conclusion that whereas the very best of talking birds such as the Indian Hill Mynah have a full equipment of resonators which can be modulated to form vowel sounds, the inferior ones lack control of the third and probably also the fourth.

As I have said, the anatomical account of the bird vocal apparatus is not sufficient to enable us at this stage to do more than guess at the three resonant cavities which must be taking part in sound production. It seems reasonable, at first sight, to assume that the main cavity is the trachea plus the syrinx, although when we consider that the trachea is particularly well designed, as Rüppell (1933) showed, for modifications in length and shape to be effected, it may be that this is primarily responsible for the second formant of the vowel. If, however, we assume that there are one or two resonating cavities below the superior larynx we must then, I think, assume that the superior larynx itself acts as another in many forms ; and quite possibly, especially in the parrots with their highly developed tongues, the mouth with or without the nasal cavities is another. Only after much further research will it be possible to be precise about such points as these. Nevertheless, these latest results have made it quite clear that within the group Aves some vocal organs can be found which function after the manner of a wind instrument having a resonating chamber with rigid walls and others after the manner of the human voice, where the vocal cords dictate and modulate the fundamental and the cavities conform.

SUMMARY

1. The present state of knowledge as to the mode of action of bird vocal organs is briefly surveyed. It is concluded that the vocal apparatus of many

of the more primitive birds acts in many respects like a wind instrument in which the resonators can be modulated and thereby master the vibrating structure (the reed). By contrast the syrinx of many song birds can be usually compared to the human vocal apparatus in its mode of action.

2. Recent studies by means of the sound spectrograph show that some song birds (*Toxostoma rufum, Acrocephalus scirpaceus, Hylocichla mustelina*) may have two or more vibrators operating independently at the same time. It is suggested that these could be two sets of tympaniform membranes, the semi-lunar membrane and structures in the superior larynx.

3. Sound spectrograms of a talking Indian Hill Mynah (*Eulabes religiosa*) show that this species at least can, when imitating human speech, produce true vowels having the same main formants as those of humans. This means that such birds must have three separately modifiable resonant chambers which correspond functionally to the human pharyngeal, oral and nasal cavities.

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THE PHYLOGENY OF *SMINTHILLUS LIMBATUS* AND THE STATUS OF THE BRACHYCEPHALIDAE (AMPHIBIA SALIENTIA)

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(With 4 plates and 18 figures in the text)

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INTRODUCTION

The genus *Sminthillus* was described by Barbour & Noble (1920) who, in the belief that its shoulder girdle is of the firmisternous pattern, allocated it to the Ranidae. Noble (1922), after a re-examination of the pectoral region in both *Sminthillus limbatus* and *S. peruvianus*, concluded that the girdle falls into neither the arciferous nor the firmisternous categories distinguished by Cope (1864, 1865) and Boulenger (1882) but that, both morphologically and functionally, it constitutes an exact intermediate between these two extremes with its epicoracoid cartilages fused anteriorly but free and overlapping posteriorly. Parker (1926) described this arcifero-firmisternous condition also in *Sminthillus brasiliensis*, the only other known species of the genus.

In the earlier work (1922) and in subsequent investigations (1926, 1931) Noble suggested that the ancestry of *Smithillus* should be sought in the bufonoid *Eleutherodactylus* (or *Syrrhophus*) from which he considered it had arisen by progressive antero-posterior fusion of the epicoracoid cartilages. He, consequently, placed *Sminthillus* in a new family, the Brachycephalidae. Barbour (1930, 1937) contested this derivation and even queried the validity of the genus which he considered to be "essentially a *Phyllobates* in all important respects".

Sminthillus has interest not only because of the problem of its ancestry but because of its inclusion within the enigmatic Brachycephalidae. This is an assemblage which Noble (1926, 1931) considered to have originated and evolved entirely within the American tropics and to which, paradoxically, he referred as "a natural even though composite family". Davis (1936) and Griffiths (1954 b) questioned the monophyletic nature of the group and emphasized that the "family", as at present defined, should have its geographical range extended to include the West African *Didynamipus* and the East Indian *Cacophryne*. If this step is taken then the latter genus, in particular, poses a distinct problem in zoogeography (Darlington, 1948, 1957, and Griffiths, 1954 b).

With the exception of Noble's (1922) brief comments on the topography of the shoulder girdle and the procoelous nature of the vertebral column, no information is available on the morphology of *Sminthillus limbatus*. This may be due as much to the animal's minute size as to relative rarity of the species in museum collections. However, it is clear that in the absence of such information, no phylogenetic analysis is possible. The aim of the present investigation was, therefore, to

(*a*) examine selected aspects of the morphology of *Sminthillus limbatus*,

(*b*) evaluate some of the taxonomic criteria employed by various authors in defining certain salientian categories,

(*c*) consider the phylogeny of the genus *Sminthillus*,

(*d*) review the relationships of the various brachycephalid groups and the validity of the family as defined by Noble (1931).

METHODS

Skeletal morphology was studied by the transparency technique (Griffiths, 1954 a) except that maceration was effected in alcoholic potash and the specimens cleared and stored in pure ethane diol. This was supplemented by serial sections and reconstructions made either by the wax plate method or that of Pusey (1939).

Myological investigations of the larger species were performed under the binocular dissecting microscope and serial sectioning was employed only to clarify doubtful points of origin and insertion. In the case of the smaller species (e.g. *Sminthillus* which may measure only 8 mm. from snout to vent) interpretation was based almost entirely on reconstructions. In nearly every instance, at least one specimen of each sex was examined from every species considered.

THE MORPHOLOGY OF *SMINTHILLUS LIMBATUS*

A. *Thigh musculature*

The pattern (Fig. 1) agrees in detail with that which Noble (1922) defined for the Procoela : both sartorius and adductor longus are present ; the semitendinosus lies deep within the thigh complex and its tendon, which receives that of the sartorius, runs ventral to and remains distinct from the gracilis major and minor.

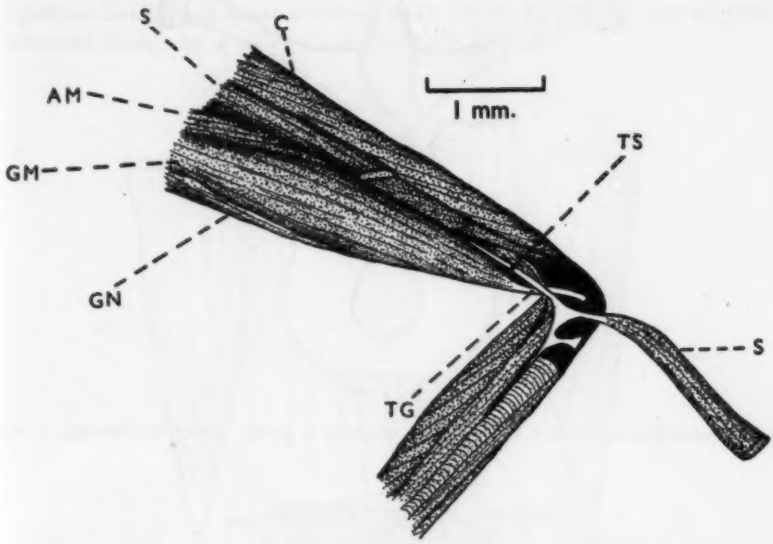

Fig. 1.—*Sminthillus limbatus.* Ventral view of thigh complex. (Key to lettering, p. 486.)

B. *Shoulder girdle*

The present investigation disagrees with the extent of epicoracoid fusion described and figured by Noble (1922, 1931). The latter author claimed that the cartilages were united for over half their length. Serial sections, however, show that the precoracoid bridge is only slightly deeper than in a generalized leptodactylid (Fig. 2). Nevertheless, the situation does differ from that of a typical arciferous girdle in that, subsequent to separating, the epicoracoid factors do not immediately overlap but run edge to edge for about one-fifth of the zonal length (Fig. 2 and Pl. 1, fig. 1). From this point the left epicoracoid broadly overlies the right up to the level of the coracoid elements where the two cartilages diverge (Figs. 2 and 3).

The sternum is cartilaginous throughout. Anteriorly, it consists of a dorsal and a ventral blade connected along the midline by a cartilaginous isthmus on either side of which a groove is consequently defined (Fig. 3 and Pl. 1, figs. 2 and 3). From the point of divergence the epicoracoid cartilages insert one into each of these grooves through which they continue as epicoracoid

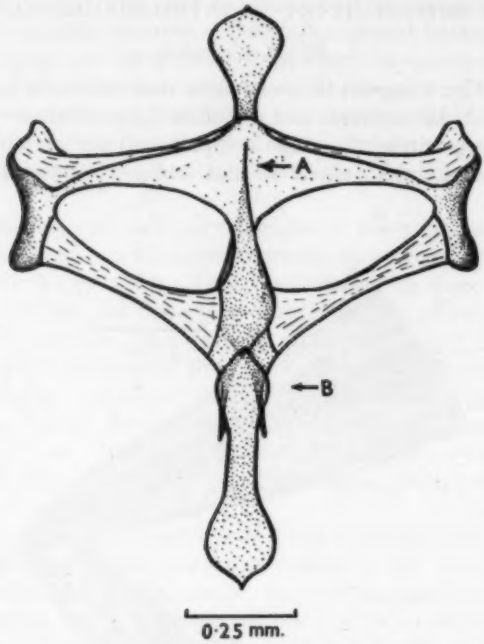

Fig 2.—*Sminthillus limbatus*. Ventral view of pectoral girdle. (Key to lettering, p. 486.)

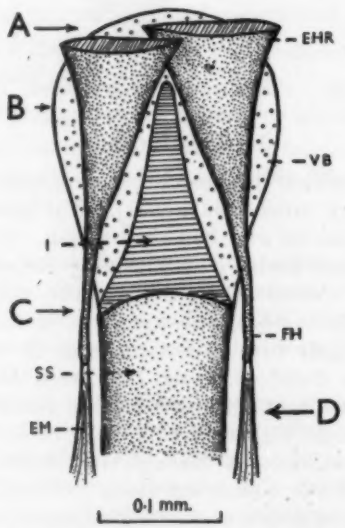

Fig. 3.—*Sminthillus limbatus*. Dorsal view of zono-sternal articulation with dorsal sternal blade removed. (Key to lettering, p. 486.)

horns and emerge to run independently alongside the sternal stem to a point one-third of the way along the latter's length (Figs. 2 and 3 and Pl. 1, fig. 3). The posterior extremity of each epicoracoid horn gives rise to a muscle that continues lateral to the sternal stem up to the cartilaginous sternal plate (Fig. 3 and Pl. 1, fig. 4). At this point the two muscles bend dorsal to the plate and unite near its posterior tip (Fig. 4). This compound muscle then extends posteriorly where it merges with the rectus abdominis about 1·5 mm. anterior to the vent (Fig. 4).

Anteriorly an expanded cartilaginous prezonal plate extends beneath the postero-medial processes and the body of the hyoid and unites with the precoracoid bridge by a short unossified stalk (Fig. 2).

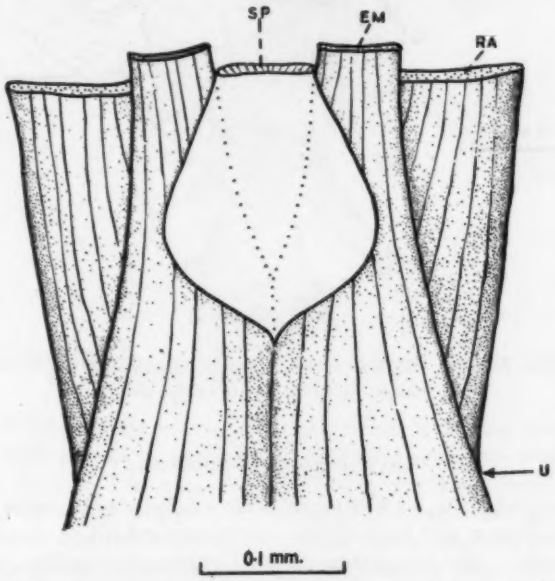

Fig. 4.—*Sminthillus limbatus*. Ventral view showing the union of the epicoracoid horn muscles with those of the abdominal recti. (Key to lettering, p. 486.)

C. *Depressor mandibulae*

This muscle has a double origin consisting of

(*a*) an anterior factor arising from the postero-dorsal edge of the squamosal stem and the posterior surface of the annulus tympanicus (Fig. 5) and

(*b*) a posterior band originating from the dorsal fascia overlying the dorsal border of the supra-scapula.

The former is rather more powerful and the latter less expanded than in the condition described by Griffiths (1954 b) for his Group *b* category. Both, however, unite typically to insert into the mandibular ramus. Also, as in all members of the above category, the angle defined by the squamosal and the mandibular ramus lies between 45 and 50 degrees.

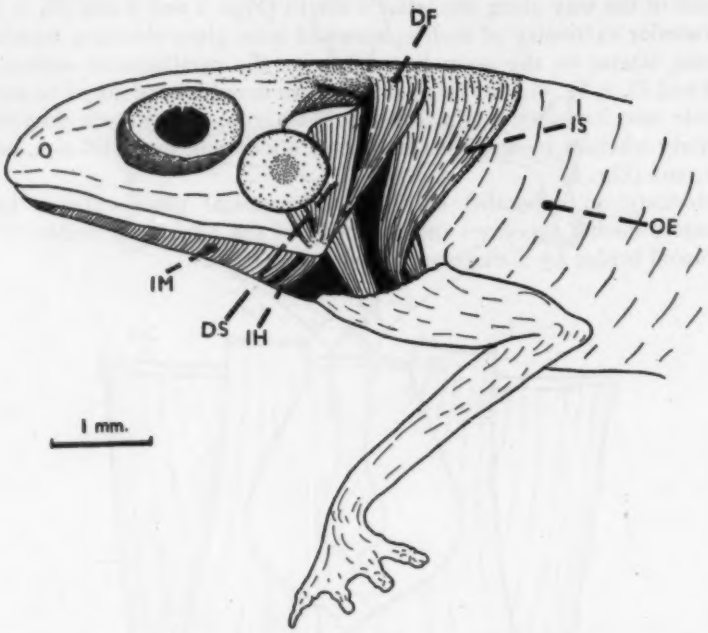

Fig. 5.—*Sminthillus limbatus*. Lateral view showing the condition of the depressor mandibulae muscle. (Key to lettering, p. 486.)

D. *Hyolaryngeal apparatus*

The hyoid plate (Fig. 6) is elongate with a length/width ratio of 2·3. Alary processes are absent and each hyale continues forward to form an extensive anterior process. The hyoglossal sinus is extremely shallow, its sides being bordered entirely by the anterior processes. Short, slender postero-lateral processes lie immediately in front of and parallel to the slim bony shafts of the postero-medial processes and the latter expand into relatively extensive cartilaginous epiphyses (Fig. 7).

The arytenoid cartilages are extremely gibbous in lateral view and triangulate dorso-ventrally. From their postero-medial apices distinct fibrous dorsal and ventral pulvinaria vocale support the vocal chords (Fig. 8 ; Pl. 2, fig. 6).

The cricoid (Figs. 7 to 9) forms a complete cartilaginous ring articulating with the arytenoid by paired ventral articular processes. Its main body is attached to both the arytenoid and the postero-medial elements by, respectively, paired crico-arytenoid and hyo-cricoid ligaments. A number of processes extend backwards from the cricoid ring. Dorso-medially an unpaired oesophageal process runs in the dorsal bronchial wall and is intimately attached to the oesophagus along the latter's midline (Figs. 7 to 9). This process ends just behind the level of the bronchial fork. In the ventral midline,

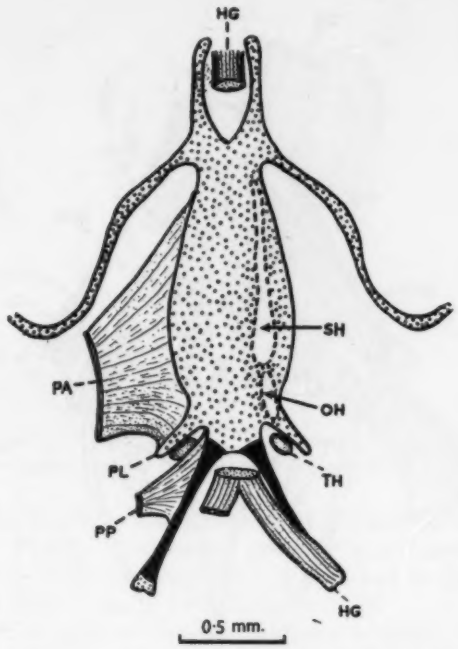

Fig. 6.—*Sminthillus limbatus*. Ventral view of hyoid plate. (Key to lettering, p. 486.)

immediately overlying the conus, lies a short, blunt cardiac process. This is bordered on each side by a pair of slim bronchial processes which run in the ventral wall of each bronchus and terminate slightly anterior to the free end of the oesophageal process. The above cartilages are present in both sexes. The male has, in addition, a pair of thick tracheal processes which extend back from the inner border of the cricoid ring and project freely into the tracheal lumen (Pl. 2, fig. 7). When the arytenoid cartilages are pulled backwards by contraction of the constrictors, their dorsal apices fit inside the cricoid ring and articulate with the bases of these tracheal processes. The latter, consequently, control the lower tensional limits that can be effected in the vocal chords (Pl. 2, figs. 5 and 7).

The *dilator laryngis* muscle (Figs. 7 and 8) originates from both the dorso-lateral edge of the cricoid ring and the dorsal surface of the postero-medial process. The two factors unite and insert just behind the pharyngeal apex of the arytenoids.

Three sets of laryngeal constrictors are present. First, a *constrictor laryngis externus* arises from the postero-medial process immediately in front of the dilator and loops ventrally around the arytenoid apices (Figs. 7 and 8 ; Pl. 2, fig. 7). There is no suggestion that the complex is paired and no evidence of a pre-arytenoid raphe as occurs characteristically in the majority of Salientia. Secondly, a *constrictor anterior* spreads strapwise from a median raphe and

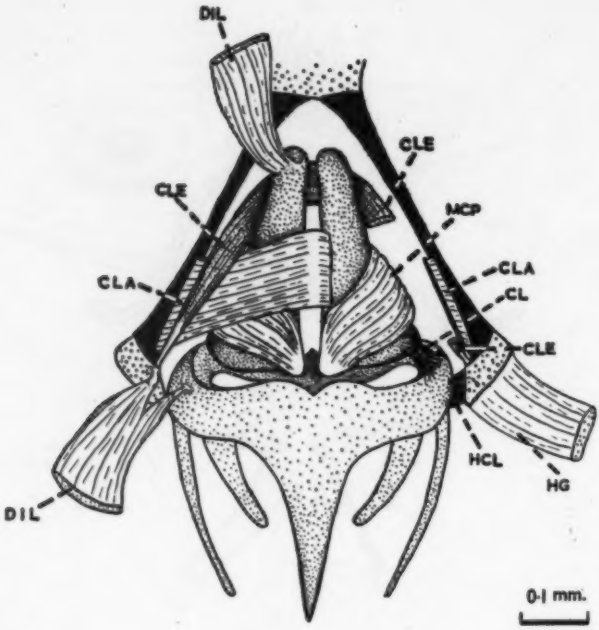

Fig. 7.—*Sminthillus limbatus*. Dorsal view of the male laryngeal apparatus. The ligaments are figured only on the right-hand side and the hyoglossus is reflected upward. (Key to lettering, p. 486.)

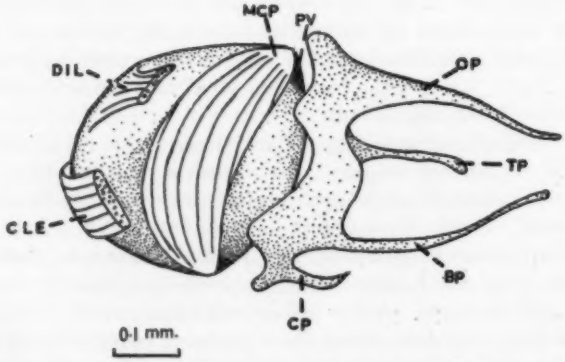

Fig. 8.—Lateral view of the larynx in the male *Sminthillus limbatus*. (Key to lettering, p. 486.)

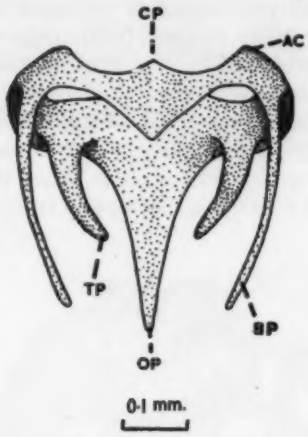

Fig. 9.—Ventral view of the cricoid in the male *Sminthillus limbatus*. (Key to lettering, p. 486.)

passes beneath the *constrictor externus* to insert on the inner edge of the postero-medial process. Finally, a *constrictor posterior* is intimately applied to the postero-lateral face of the arytenoid and, at each end, is attached to a fibrous pulvinare vocale (Figs. 7 and 8 ; Pl. 2, figs. 5 to 7).

The *petrohyoideus anterior* muscle originates typically on the otic arcade and inserts along the edge of the hyoid body from the tip of the postero-lateral process to just behind the hyalial junction (Fig. 6). It is innervated by the glossopharyngeal nerve. The posterior petrohyoideal complex is reduced to a single muscle arising from the anterior half of the bony shaft of the postero-medial process. Innervation is by the vagus and this single muscle presumably represents the anterior of the three members present in most Salientia.

The pattern of the remaining hyolaryngeal musculature is essentially that of a generalized anuran type as exemplified by *Leptodactylus ocellatus* (Trewavas, 1933). It should be noted that, as in the latter species, the *hyoglossus* in *Sminthillus*, also, inserts directly on the ventral surface of the postero-medial process (Figs. 6 and 7).

E. *Urogenital system*

The following account is based on an examination of fourteen individuals of which eight were females.

The male system conforms exactly to the eleutherodactylid pattern described by Bhaduri (1953) ; all traces of Mullerian ducts are absent, there is no evidence of a urogenital sinus, a pair of moderately sized seminal vesicles are present and the Wolffian ducts unite immediately adjacent to the cloaca.

The female system of *Sminthillus limbatus* (Figs. 10 and 11) is unique among all salientian forms hitherto described in that only the right Mullerian duct is present as a functional unit, the left being reduced to a vestige. The right ostium is large and opens into a short *pars recta* which, almost immediately,

leads into a greatly coiled *pars convoluta* traversed by extensive dilatations. Both regions are histologically similar, consisting of an outer adventitia of connective tissue with a thin muscularis of circular smooth muscle, a middle layer of large mucous cells and an inner ciliated epithelium with many goblet cells opening into the oviducal lumen. The left vestigial Mullerian duct extends for only about 0·25 mm. anterior to the common ovisac (Fig. 10 ; Pl. 3, fig. 9). Topographically the vestige is a hollow cone which differs histologically from the functional duct in not possessing the middle mucous layer. Its epithelium is also unconvoluted.

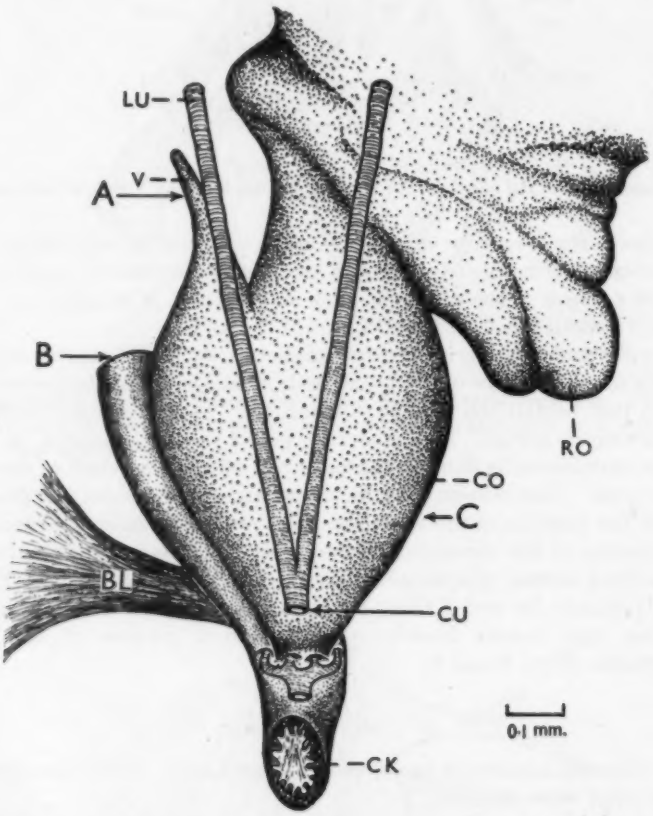

Fig. 10.—*Sminthillus limbatus*. Dorsal view of the terminal portion of the female genital tract. (Key to lettering, p. 486.)

The two oviducts open into a common ovisac (uterus of Gaupp, 1904 and Bhaduri, 1953) whose wall, like that of the vestigial duct, consists only of two layers representing the outer adventitia and the inner epithelium of the functional oviduct. The middle mucous layer of the latter, however, does extend a short distance into the right ovisac floor forming a wedge-shaped

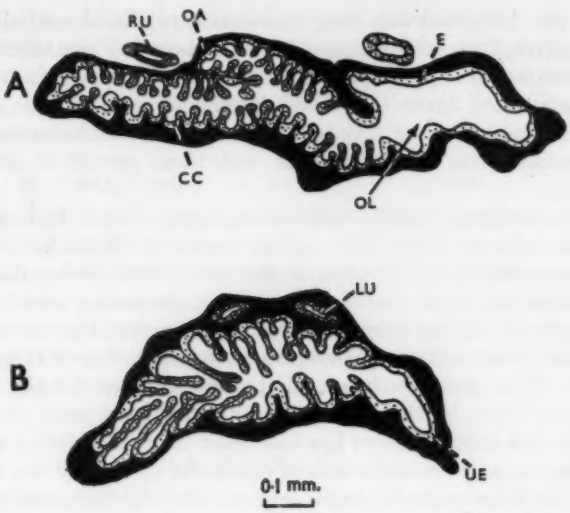

Fig. 11.—Transverse sections through levels B and C of Fig. 10. (Key to lettering, p. 486.)

tract (Fig. 12 D). As this tract tapers posteriorly so, concurrently, do the over-all dimensions of the mucous cells of which it is composed diminish until ultimately they completely disappear (Fig. 11 ; Pl. 4, fig. 12).

The right half of the ovisac is thrown into highly vascular longitudinal folds throughout its entire length. The left side, on the other hand, has an area where the epithelium is smooth and completely devoid of ridges (Pl. 3, fig. 10). Anteriorly, this unfolded area occupies exactly the right half of the sac lining (Fig. 11) ; posteriorly, the tract tapers and disappears some distance before the genital chamber opens into the cloaca (Fig. 12). The distinction between the two regions is always sharp and, at no level is there any indication of a gradual transition from one condition to the other.

The preceding account of the female tract is based on its condition during the breeding season.

Bhaduri (1953) schematized the ovisac (uterine) variations in the Salientia into three broad categories : *separatus*, *septatus* and *communis* (Fig. 12) according to whether the ovisacs are, respectively, (i) discrete along their entire

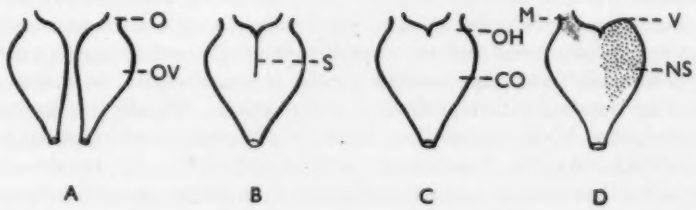

Fig. 12.—Diagrams of the chief types of ovisacs found in the Salientia. D=*Sminthillus limbatus* Fine stippling=area of the ovisac possessing a middle mucous layer ; coarse stippling=area of the ovisac insensitive to the female hormone. (Key to lettering, p. 486.)

length and open independently into the cloaca, (ii) fused medially and share a common opening into the cloaca but with their two chambers completely or partly separated by a partition, (iii) fused medially, share a common unpartitioned chamber and enter the cloaca by the same aperture. It should be noted that in neither (ii) nor (iii) does the common chamber ever incorporate the anteriormost parts of the ovisacs and these persist as discrete ovisac horns (Fig. 12).

Sminthillus limbatus clearly falls into category (iii). It must also have evolved from this or from the *septatus* condition since its origin from a *separatus* type would have resulted in the vestigial Mullerian duct communicating independently with the cloaca as in non-predatory birds.

The topography of the female system suggests that the vestige represents only the ovisac horn and that the oviduct corresponding to it has been completely lost. This view, if correct, might also account for the absence of a middle mucous layer in the vestige. Histological evidence shows that the epithelium of this vestigial horn has lost most of its sensitivity to the female gonadal hormones and the same lack of reactivity shown by the smooth tract in the left half of the main chamber suggests that the tissue which constitutes this tract represents the contribution of the left Mullerian duct to the common ovisac. The fact that the tract no longer extends to the cloaca in the adult is probably due to an allometric growth pattern. It should be emphasized that, although the tissue contributed by the left Mullerian duct no longer forms vascular folds in response to the female hormone, some degree of reactivity persists, for during the non-breeding season it regresses with the remainder of the reproductive tract.

The selection pressure concerned in the vestigiality of the oviduct in *Sminthillus*, and indeed in any craniate where this phenomenon has occurred, was probably the progressive increase in the value of the ratio E/C, where E represents the diameter of the ovulated egg and C the minimum width of the coelom between the ostia and the cloaca. When this value exceeds 0·5 (and in *Sminthillus* it is 0·7) and the two ostia occupy approximately the same level along the antero-posterior axis, there is a real possibility of two eggs, one in each oviduct, impacting and thus effectively blocking the ducts. This can be averted in a number of ways. Firstly by an exaggerated staggering of the ovary and ostium of one side with those of the other so that all the eggs in the shorter oviduct lie in a discrete line caudad to the first egg discharged from the anteriormost ovary This condition obtains in most snakes and in coecilians but, clearly, it can only occur in long-bodied forms with the requisite length of general coelom to permit the degree of staggering involved. A second solution is to suppress one ovary as has occurred in many sharks, birds and in the duckbilled prototherian mammals. Finally, as in the case of non-predatory birds, *Sminthillus limbatus* and some typhlopid snakes, one of the oviducts may be functionally eliminated. (The Typhlopidae, unlike most ophidia, have their ovaries and ducts compacted immediately anterior to the cloaca.) The occurrence of the same solution in the widely different groups is clearly due to convergence arising from the common problem of macrolecithy.

Sminthillus brasiliensis retains two functional oviducts. It is, however, a larger frog than the Cuban species (18 mm. snout to vent) with an *E/C* value of slightly less than 0·4. No female specimens of *Sminthillus peruvianus* were available for examination but from Noble's account of the species (1921) oviducal reduction would not be expected according to the above argument.

EVALUATION OF TAXONOMIC CRITERIA

The scheme of classification currently employed for the Salientia is that proposed by Noble (1931). Meanwhile, evidence has accrued casting doubt on the significance of some of the criteria which this scheme uses for defining primary categories and other criteria, based on characters not employed by Noble, have been proposed. Before considering problems of phylogenetic relationships it may, therefore, be pertinent to examine briefly the validity of some of the characters to which various authors have ascribed taxonomic importance.

A. *Vertebral column*

Noble's scheme divides the Salientia into five suborders : Amphicoela, Opisthocoela, Anomocoela, Procoela and Diplasiocoela according to the nature of the vertebral centra. In essence this is an application of propositions made by Nicholls (1916). Prior to Nicholls's publication Boulenger (1908) had already rejected the diagnostic value of the vertebral column after encountering both procoely and opisthocoely within the genus *Megalophrys*. Nicholls himself found four species of *Rhacophorus* : *madagascariensis*, *maximus*, *schlegeli* and *reinwardti*, that were uniformly procoelous but he chose to regard these as " peristing forms which connect the several groups ". To this list of procoelous Firmisternia, Ramaswami (1933) added *Rhacophorus dubius*, *Ixalus chalzodes*, *I. oxyrhynchus* and *Nannobatrachus kempholensis* thus further weakening Noble's main tenet. It should also be recalled that Noble himself (1922) listed some species of *Arthroleptis* (*poecilonotus* and *variabilis*) as procoelous whilst recording *A. feae* as diplasiocoelous. During the present investigation some specimens of *Arthroleptis variabilis* were found to be procoelous and others diplasiocoelous, a plasticity which may explain the disagreement between Nicholls and Noble concerning this species. But the most important objection to the scheme came when Parker (1934) showed that no less than sixteen of the forty-three microhylid genera examined by him possess uniformly procoelous vertebrae. He emphasized that any attempt to group the genera on vertebral characters alone results in such anomalies as linking the majority of the Madagascar genera with the Papuan *Genyophryne*, *Sphenyophryne* and *Cophixalus* and allying the Madagascan *Dyscophus* with the Papuan *Asterophrys*. During this investigation the results of the above authors have been confirmed ; in addition uniform procoely was also encountered in *Rana adspersa* (B.M. No. 1861/3/20/19), *R. guttulata* (B.M. No. 1887/8/10), *R. ornatissima* (B.M. No. 1907/6/29–78), *Rhacophorus goudoti* (B.M. No. 95/1/12/25) and in ten specimens of *Arthroleptis poecilonotus*. Furthermore, a condition exists in *Philautus romeri* (Pl. 4, fig. 15) where the sacral and presacral vertebrae are fused thus making allocation to any of Noble's suborders impossible. This

synsacry occurs also in *Dendrobates* and was described by Ramaswami (1933) for *Rana curtipes*.

It is clear, therefore, that not only does the nature of the vertebral column not carry the precise taxonomic implications vested in it by Noble but the occurrence of dissimilar vertebral patterns in two groups does not, *ipso facto*, imply an absence of relationship.

B. *Thigh musculature*

In the diagnosis of families Noble (1922, 1931) attached considerable importance to the disposition of the distal tendons of the thigh muscles. He considered this character of particular significance in distinguishing the Procoela from the Diplasiocoela because (he maintained) the latter are the only group of frogs in which the tendon of the semitendinosus lies dorsal to the gracilis mass. Latsky (1930) cast doubt on the diagnostic value of this criterion when she showed that greater variation exists between the two *Breviceps* species investigated by her than between *Rana* and most of the South African microhylid genera. Parker (1940) demonstrated that the thigh complex of the Australian Leptodactylidae can be divided into four groups illustrating a perfect gradation from the bufonoid condition of the Cycloraninae, where the semitendinosus tendon lies ventral to and distinct from the gracilis mass, to the completely ranoid pattern of the Myobatrachinae. Colefax (1956) described the latter condition in the completely procoelous *Pseudophryne corroboree*. It is particularly significant that during the present investigation the ranoid pattern was found also in *Hyloxalus* (Fig. 13), the genus, according to Noble, from which both *Dendrobates* and *Phyllobates* have stemmed.

Since Noble's main argument was that " none of the Procoela have the tendon of the semitendinosus free from the gracilis mass, or, in other words, in the typical ranid condition " the above results clearly nullify much of, if not all, the taxonomic importance which he placed in the character for defining major groups. However, the constancy of the pattern in the true ranids on

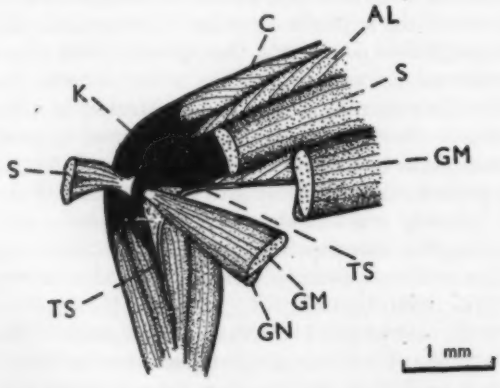

Fig. 13.—*Hyloxalus bocagei*. Ventral view of thigh complex. (Key to lettering, p. 486.)

the one hand and the true bufonids on the other and, unlike the vertebral structure, the complete absence of intra-specific variability, suggests that the nature of the thigh complex can provide useful secondary evidence in the designation of lower taxonomic categories.

C. *Pectoral girdle*

Cope (1864, 1865) was the first to grasp the taxonomic significance of the salientian shoulder girdle. Boulenger slightly modified Cope's scheme in his catalogue (1882) when he defined two major phaneroglossal groups, the Arcifera and the Firmisternia, distinguishable by the form of their pectoral girdles. The Arcifera he described as frogs " with clavicles and coracoids divergent, connected by an epicoracoid which is free from and generally overlaps the corresponding cartilage of the opposite side " and the Firmisternia as a group " with clavicles and coracoids nearly abutting in the midline and only narrowly separated by fused epicoracoids ". In distinguishing between these two basic girdle types the emphasis subsequently shifted, almost entirely, to the overlapping of the epicoracoid cartilages in the arciferous condition and their mesal fusion in the case of the Firmisternia.

The validity of the Arcifera and Firmisternia as primary groups was not queried, and no firmisternous type more closely allied to an arciferous genus than to the Firmisternia was suggested, until Noble (1922) described and figured the shoulder girdle of *Sminthillus limbatus*. He maintained that the epicoracoid cartilages are fused anteriorly for half their length and that " separation occurs only in the region of the coracoids ". This " intermediate " type of girdle, Noble argued, invalidates the value of the structure as a diagnostic character in defining major salientian categories. He envisaged a progression of this trend of epicoracoid fusion having given rise to the firmisternous stage along numerous independent lines and he referred to *Rhinoderma* as a completely firmisternous genus which should be regarded as the end-product of such an evolutionary line. In further support of his argument he quoted (1926) the larval and adult condition of the shoulder girdle in *Rana rugulosa* which, he maintained, " is fully arciferal for some time after metamorphosis " and " when adult the coracoid cartilages are fused only at their extreme anterior and posterior ends ; the greater part of the coracoid cartilages are free and overlapping throughout life ".

None of these points made by Noble are valid. Firstly, as has already been shown, the precoracoid bridge in *Sminthillus* is not significantly deeper than in any generalized leptodactylid and the epicoracoids are not, as Noble claimed, fused up to the coracoid level. Secondly, *Rhinoderma* is not firmisternal but its epicoracoid cartilages are free and overlapping in the coracoid region and they extend posteriorly, on either side of the sternum, as distinct epicoracoid horns (Fig. 14 ; Pl. 3, fig. 11). Finally, developmental studies on *Rana rugulosa* and *Rana tigrina* show that at no stage do they possess " a fully arciferal " shoulder girdle as Noble so categorically stated but the adult condition is reached long before the end of metamorphosis (Pl. 2, fig. 8).

These findings clearly necessitate a re-examination of the salientian shoulder girdle both developmentally and taxonomically. Griffiths (in MS.) has recently

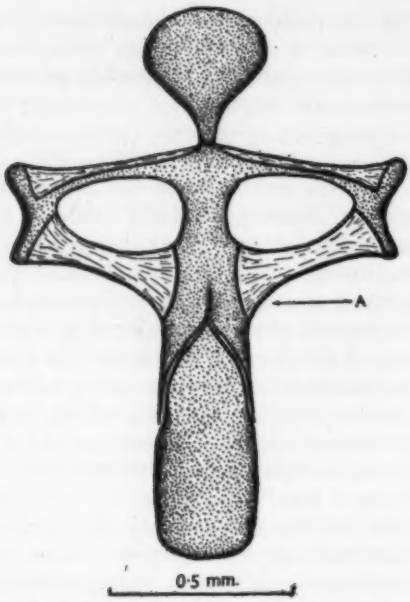

Fig. 14.—*Rhinoderma darwini*. Ventral view of the pectoral girdle with the sternum pulled slightly back from the epicoracoid horns. (Key to lettering, p. 486.)

completed such an examination and concludes that the weakness of the Cope-Boulenger system lay in the formulation of the structural criteria employed and not, as Noble suggested, in the selection of a taxonomically invalid character. It is shown that criteria based only on degree of fusion, freedom and overlapping of the epicoracoid cartilages are incapable of exact taxonomic application since they cannot accommodate the condition encountered in *Rana rugulosa* and *R. tigrina* and they wrongly allocate such genera as *Atelopus* which, on the evidence of osteology, myology and the reproductive system, are clearly allied to the Bufonidae (Griffiths, 1954 b). The author then shows that, if attention is focussed on the zono-sternal articulation, the Salientia can be precisely divided into two primary divisions according to whether or not they possess posteriorly-directed epicoracoid horns. These two groups agree broadly with, respectively, the Arcifera and Firmisternia (*sensu* Boulenger) except that such forms as *Rana rugulosa*, *R. tigrina* and *Atelopus* are correctly designated. The scheme, which will be published independently, also avoids the enigma of the "arcifero-firmisternal" condition defined by Noble (1922).

D. *Depressor mandibulae*

Griffiths (1954 b) showed that the origin of the depressor mandibulae muscle in Salientia occurs in one of three conditions :

(*a*) as a thick band arising from the posterior border of the otic arm of the squamosal (Fig. 15 A),

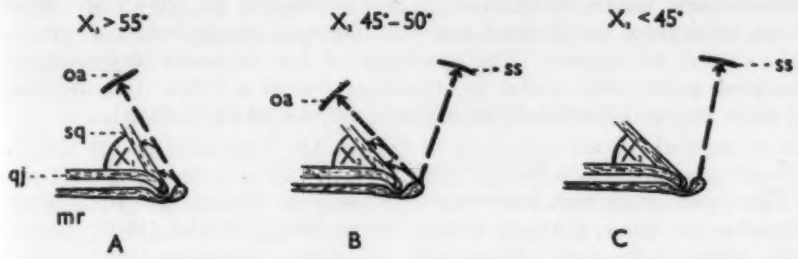

Fig. 15.—A diagram of the conditions of the depressor mandibulae muscle in the Salientia. (Key to lettering, p. 486.)

(*b*) as a wide sheet arising from the squamosal and the dorsal fascia (Fig. 15 B),

(*c*) as a single sheet arising from the dorsal fascia only (Fig. 15 C).

It was also shown that the condition of the depressor mandibulae is characteristically constant within families and that correlation exists between the muscle condition and the angle defined by the squamosal and the maxillary ramus. During the present work investigation into these relationships has been extended to include the following families and genera : Atelopodidae (*Atelopus, Brachycephalus*) ; Bufonidae (*Bufo, Nectophryne, Nectophrynoides, Pedostibes, Cacophryne, Dendrophryniscus, Oreophrynella*) ; Hylidae (*Acris, Agalychnis, Ceratohyla, Gastrotheca, Hyla, Nyctimantis, Phyllomedusa, Pseudis, Pternohyla, Tryprion*); Letptodactylidae (*Adelotus, Batrachophrynus, Calyptocephalus, Ceratophrys, Crinia, Cyclorana, Eleutherodactylus, Heleioporus, Hylodes, Hylorhina, Leptodactylus, Limnodynastes, Physalaemus, Paludicolal Pleurodema, Telmatobius, Uperoleia*) ; Ranidae (*Arthroleptis, Arthro, leptella, Astylosternus, Cacosternum, Cornufer, Dimorphognathus, Microbatrachella, Ooeidozyga, Petropedetes, Philautus, Rana, Dendrobates, Hyloxalus,-Phyllobates*) ; Microhylidae (*Asterophrys, Barygenys, Calophrynus, Genyophryne, Glyphoglossus, Hypopachus, Kalophrynus, Kaloula, Microhyla, Phrynomerus, Plethodontohyla, Rhombophryne, Uperdon*) ; Discoglossidae (*Alytes, Bombina, Bombinator, Discoglossus*); and Pelobatidae (*Megophrys, Pelobates, Pelodytes, Scaphiopus*). The results are summarized in Table 1 and it will be noted

TABLE 1

Family	Numbers examined			Squamosal angle		Condition of depressor mandibulae
	Genera	Species	Specimens	Range	Mean	
Atelopodidae	2	11	158	(65–70)	68	*a*
Bufonidae	7	41	262	(55–68)	64	*a*
Hylidae	10	34	120	(45–50)	49	*b*
Leptodactylidae	10	41	166	(45–50)	49	*b*
Ranidae	11	61	248	(45–50)	48	*b*
Rhacophoridae	4	14	46	(45–50)	49	*b*
Microhylidae	13	18	91	(45–50)	49	*b*
Discoglossidae	4	7	58	(38–45)	41	*c*
Pelobatidae	4	11	38	(40–45)	41	*c*

that the angle values lie between 55 and 70 degrees for Group *a*, between 45 and 50 degrees for Group *b* and that Group *c* species rarely attain and never exceed 45 degrees. The condition of the depressor mandibulae is considered particularly useful in separating Group *a* forms (the Bufonidae and their atelopodid offshoot) from the remainder of the Salientia.

E. *Hyolaryngeal apparatus*

The most important comparative studies on the anuran hyolaryngeal apparatus are those of Duges (1835), Henle (1939), Wilder (1892), Goppert (1895, 1898), Edgeworth (1920) and, especially, Trewavas (1933). In an exhaustive survey of the skeleton and muscle of the hyoid and larynx the latter author showed that, from a phylogenetic point of view, two groups are particularly well characterized by the nature of their hyolaryngeal complex :

(i) the Bufonidae (Bufoninae of Noble, 1931) and the genera *Atelopus*, *Dendrophryniscus* and *Oreophrynella*,

(ii) the Ranidae and the Rhacophoridae.

The former are distinguished by the absence of both pulvinaria vocale and their associated muscles the *constrictor laryngis posterior* and, also, by the curving of the *hyoglossus* muscle around the postero-medial edge of the postero-medial process to insert on the dorsal surface of the latter rather than on the ventral as is usual in other forms. The second group is distinct from all others (except *Hemisus* and one species of *Breviceps*) in possessing a *cartilago apicalis* to the arytenoid. This latter character must be of comparatively recent evolution since it is absent in the microhylid genera which are, indisputably, of ranoid descent.

It is clear, therefore, that the hyolaryngeal structure provides important confirmatory evidence in the analysis of group affinities where categories (i) and (ii) noted above, are involved. It is interesting, and perhaps significant, that the discreteness of the bufonid/atelopodid line is emphasized by the nature of both squamoso-mandibular and the hyolaryngeal apparatuses.

F. *Urogenital system*

Spengel (1876) and Bhaduri (1951) are the chief workers to have dealt comparatively with the salientian urogenital system. The results of both these investigators suggest that the system has no great significance for defining major taxonomic categories. Relative to the present discussion, however, it should be noted that Bhaduri records the Wolffian ducts as uniting adjacent to the cloaca in all leptodactylids examined by him, whereas in both *Phyllobates* and *Dendrobates* the ducts open separately.

Davis (1936) considered the presence of the organ of Bidder to be a universal feature of the genera *Bufo*, *Nectophrynoides*, *Pedostibes* and *Pseudobufo*. Griffiths (1954 b) confirmed Davis's findings for the above genera and also reported the occurrence of the organ in *Atelopus*, *Cacophryne*, *Dendrophryniscus* and *Nectophryne*. He emphasized that, although the presence of the organ of Bidder in a species should be regarded as proof of bufonid affinities, the absence of the structure need not, in itself, establish that such affinities do not exist. He quoted the evidence of embryology and ontogeny, both of which

indicate that Bidder's organ is a vestigial structure whose "degeneration and even disappearance would not be unexpected either ontogenetically or phylogenetically".

THE PHYLOGENY OF *SMINTHILLUS LIMBATUS*

Noble (1926) considered the arrival of *Bufo* into South America as too recent for the genus to constitute a possible ancestral stock for the Brachycephalidae. Consequently, since he regarded the latter as having evolved and radiated entirely within the American tropics, he sought their origins among the leptodactylid genera only. But Shaeffer (1949) described *Neoprocoela edentatus* from the early Tertiary of Patagonia with strong skeletal resemblances to the bufonid/atelopodid group. Furthermore, Parker (1934) and Griffiths (1954 b), from the evidence of osteology, myology and the condition of the genital system, concluded that the ancestry of the brachycephalid genera *Cacophryne* and *Didynamipus* should be sought, respectively, in the stocks of *Pedostibes* and *Nectophryne*. Griffiths demonstrated, also, that the latter two genera are true bufonids (Bufoninae of Noble). Consequently, discussions on the phylogeny of brachycephalid forms should consider possible relationships, not only to eleutherodactylid and phyllobatid lines as proposed by Noble (1922, 1926) and Barbour (1930, 1937), but also to the Bufonidae *sensu stricto*.

Table 2 compares various selected characters of *Sminthillus limbatus* with those of the possible ancestral lines mentioned above. The sequence of tabulation indicates the present author's assessment of the taxonomic importance of the criteria employed.

Phyllobates is clearly excluded from being the stem stock because its shoulder girdle lacks epicoracoid horns. This conclusion is supported by the subsidiary evidence of the discrete nature of the Wolffian ducts and by the

TABLE 2

Character	*Sminthillus*	Leptodactylidae (*Eleutherodactylus*)	Dendrobatidae	Bufonidae
Epicoracoid horns	+	+	—	+
Arcifery	+	+	—	+
Thigh complex	B	B	(R—I)	B
Depressor mandibulae	*b*	*b*	*b*	*a*
Squamosal angle	50°	50°	50°	55°>
Pulvinaria vocale	+	+	+	—
M. constrictor laryngis posterior	+	+	+	—
Insertion of *m. hyoglossus*	V	V	V	D
Vertebral column	P	P	(P—Sy)	P
Prezonal	+	+	+	—
Bidder's organ	—	—	—	+
Wolffian ducts	U	U	S	U
Bursa angularis oris	—	—	+	—

Abbreviations: *a*, *b*,—condition of depressor mandibulae as shown in Fig. 15; B—bufonid pattern; D—dorsal I;—pattern intermediate between B and R but closer to the latter; P—procoelous; R—ranoid pattern; S—separate; Sy—synsacral; U—united; V—ventral.

pattern of the thigh complex (Fig. 16) in which the tendon of the semitendinosus lies dorsal to the massive gracilis major but ventral to the much smaller gracilis minor. It is also noteworthy that both *Phyllobates* and *Dendrobates* possess a *bursa angularis oris* (" Mundwinkeldrüse " of de Villiers, 1931). This structure is absent in *Sminthillus* and its nature and significance will be discussed later.

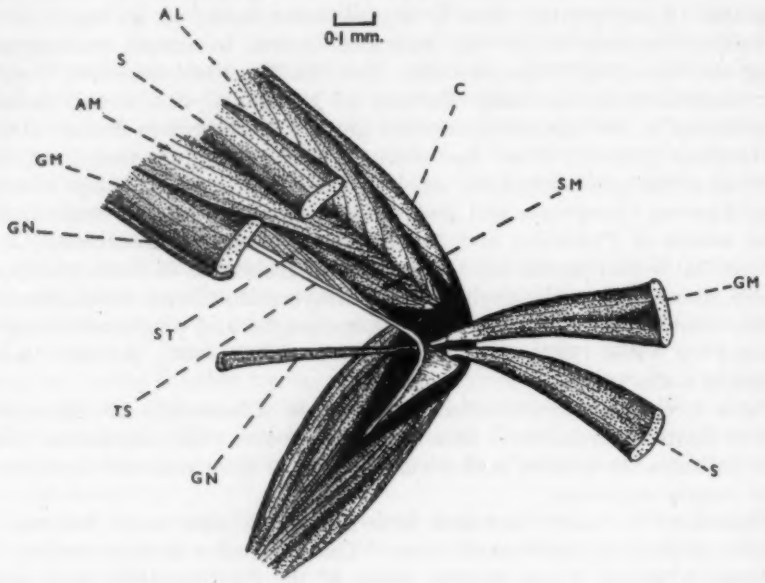

Fig. 16.—*Phyllobates trinitatus*. Ventral view of thigh complex. (Key to lettering, p. 486.)

Equally clearly the ancestry of *Sminthillus* should not be sought among the Bufonidae (Bufoninae of Noble). This is indicated by the pattern of the hyolaryngeal apparatus and its associated musculature, by the nature of the depressor mandibulae and, to a lesser degree, by the absence of an organ of Bidder.

Eleutherodactylus, on the other hand, has all the characters expected of a parental stock and differs morphologically from *Sminthillus* only in the female reproductive system, the specialized nature of which in the latter genus has already been discussed. Furthermore, if in the analysis of salientian relationships, life history data have the importance which is generally assigned to them (Noble, 1926, 1927, 1931), then the breeding habits, reduction of egg number and direct development of *Sminthillus* (Dunn, 1926) support an eleutherodactylid origin.

The inter-relationships of the three species (*brasiliensis*, *limbatus* and *peruvianus*) currently referred to *Sminthillus* may be interpreted in one of two ways. Firstly, they may be regarded as members of a natural group which

once occupied an extensive range but are now restricted, respectively, to localities in the Organ Mountains of Brazil, Cuba and Southern Peru. Secondly, they may be considered an essentially polyphyletic assemblage representing three independent offshoots of eleutherodactylids in these localities. Hitherto, the main support for the first proposition has been the occurrence in all three forms of an " arcifero-firmisternal " shoulder girdle (Parker, 1926). But as has already been indicated, the degree of epicoracoid fusion is no longer tenable as a character for defining primary groups (Griffiths, in MS.). Furthermore, it has been demonstrated (Parker, 1934; Griffiths, 1954 b) that this " arcifero-firmisternal " condition has been independently evolved in at least two other genera : the African *Didynamipus* and the East Indian *Cacophryne*. It should also be emphasized that the geographically intermediate *Sminthillus brasiliensis* can in no way be considered a morphological link between the other two species (Parker, 1926). The present author, consequently, concludes that the three species should be regarded as convergent forms independently evolved from different eleutherodactylid stocks. A case thus exists for the adoption of Barbour's suggestion (1930) that the Peruvian form be generically designated *Noblella*. For the same reasons the generic name *Euparkerella*, type *E. brasiliensis* (Parker), may be suggested for the Organ Mountain species with the retention of *Sminthillus* for the Cuban forms only.

These genera are easily distinguished from the Bufonidae by their depressor mandibulae, their hyolaryngeal apparatus and the presence in them of a prezonal element, and from the Hylidae by their lack of intercalary phalanges. The results of the present investigation, particularly concerning the taxonomic validity of the shoulder girdle, clearly leaves no basis for separating them from the Leptodactylidae. I therefore propose that *Noblella*, *Euparkerella*, and *Sminthillus* be removed from the Brachycephalidae and re-allocated to the Leptodactylidae.

THE STATUS OF THE BRACHYCEPHALIDAE

Noble (1931) argued that the " Brachycephalidae may be considered a natural though composite family " consisting of three subfamilies, Rhinodermatinae, Dendrobatinae and Atelopodinae, each having arisen " from a different stock of bufonids . . . residing in the same general area ". Davis (1935) and Griffiths (1954 b) contested this view and emphasized that, according to modern taxonomic principles, lines independently evolved from different groups of a single family must either be retained as categories within the parent family or each separately accorded full family status. Neither convergence of the derived lines nor the fact that the ancestral stocks resided in the same general regions can influence this step in any way. These authors, therefore, proposed that the Rhinodermatinae, Dendrobatinae and Atelopodinae be elevated to full family rank.

A. Atelopodinae

The Atelopodinae include the South American genera *Atelopus*, *Brachycephalus*, *Dendrophryniscus* and *Oreophrynella*, the West African *Didynamipus* (Parker, 1931) and the East Indian *Cacophryne* (Griffiths, 1954 b). The

presence of Bidder's organ in all these forms (except *Brachycephalus*, Table 3) makes their origin from the Bufonidae (*sensu stricto*) indisputable. Their kinship to the latter family is further reflected in the condition of the depressor mandibulae, the lack of a prezonal element in the pectoral girdle, the hyolaryngeal apparatus and the thigh complex. They differ from the parent stock chiefly in the fact that the epicoracoid cartilages are fused along their mesial edges : from the precoracoid to the posterior edge of the coracoid in *Atelopus* and *Brachycephalus* and for a short distance behind the precoracoid bridge in the other genera.

TABLE 3

Genus	Species	Bidder's organ		No. of individuals examined
		Juvenile males	Mature males	
Atelopus	*cruciger*		+	1
	elegans	+ (3)	+ (6)	9
	flavescens	+ (1)	+ (3)	4
	gracilis		+	2
	ignescens	+ (2)	+ (12)	14
	longirostris		+	2
	oxyrhynchus		+	1
	pulcher		+	1
	varius	+ (4)	+ (20)	24
	zeteki	+ (6)	+ (22)	33
Brachycephalus	*epihippium*		—	5
Cacophryne	*borbonica*	+ (1)	+ (12)	15
			— (2)	
Dendrobates	*tinctorius*		— (4)	4
Dendrophryniscus	*stelzneri*	+ (3)	— (2)	7
			+ (2)	
Oreophrynella	*quelchi*	+ (1)	— (4)	6
		— (1)		
Phyllobates	*latinasus*	— (2)	— (6)	8
	subpunctatus	— (1)	— (2)	3
	trinitatus	— (1)	— (7)	8
Rhinoderma	*darwini*	— (2)	— (4)	6
Sminthillus	*limbatus*	— (1)	— (4)	5

The East Indian *Cacophryne* possesses a complete ear apparatus and the squamosal arm is supra-otic, as in the true Bufonidae, and the genus should be considered as representing a distinct evolutionary line with its origin in the geographically-close *Pedostibes* (Griffiths, 1954 b). The African and South American species resemble each other and differ from both *Cacophryne* and the parent family in not having a tympanum, cavum, columella, tympanic ring etc. and in possessing a latero-otic squamosal arm. Parker (1934) and Griffiths (1954 b) regarded these resemblances as too detailed to be accounted for by convergence. This is now considered a misinterpretation since a current investigation by the present author shows that, during development, the ear apparatus in a range of both African and South American bufonids passes through exactly the conditions just described for *Didynamipus* and the New

World atelopodids. The character is thus a paedomorphic one and its occurrence in such forms as *Liopelma*, *Bombina*, *Pelobates*, *Melanobatrachus*, *Hoplophryne* etc. indicates that it is of relatively common occurrence in the Salienta*. I would suggest, therefore, that the South American and the African atelopodids represent two distinct lines independently evolved from different bufonid stocks residing in the same general area as is now occupied by their respective offshoots. For the African genus a nectophrynid stem stock is indicated (Griffiths, 1954 b) whilst the osteology, myology and urogenital system etc. of the New World forms points to *Bufo* as the ancestor. Noble's argument that the latter genus is too recent an arrival in South America is no longer so weighty, since Schaeffer (1949) described *Neoprocoela edentatus* from the Lower Oligocene of Patagonia. Furthermore, it should be recalled that the fossil history of the Bufonidae in South America is not significantly less ancient than it is in Africa. In any event, failure to discover the fossil remains of a particular animal group in no way proves that the group never existed in a particular area, and such negative evidence should only be applied with much reserve in the analysis of evolutionary and dispersal patterns.

This view that the atelopodids represent paedomorphic off shoots of bufonid stocks is supported by the high value of the squamosal angle in these forms (Table 1), for measurements of this angle during development in *Bufo*, *Rana*, *Hyla*, *Microhyla*, *Leptodactylus* and a number of other genera show that the squamosal, when it begins its backward migration, lies at right angles to the upper jaw. Towards the end of metamorphosis, when its migration is completed, the squamosal rotates and slopes forward so that the squamosal angle gradually diminishes and the adult condition is reached (Table 4). The adult value in *Atelopus* etc. thus represents the late metamorphic condition in *Bufo* (Table 4, Pl. 4, fig. 14). The relatively high value of the squamosal angle in the Bufonidae themselves when compared with other families suggests that some degree of paedomorphy has occurred in them, too. This suggestion is supported by the fact that, during the later stages of metamorphosis, leptodactylids, hylids, ranids and rhacophorids pass through that condition of the depressor mandibulae which characterizes the adult bufonids (Table 1, and Fig. 17). The edentulous condition of the Bufonidae and the persistence of the mesogonad as an organ of Bidder may be similarly interpreted. The paedomorphy displayed by the atelopodids is thus but a progression of a trend already evident in the parent family.

The three derived atelopodid lines must now either be retained as categories within the parent family or, if it is considered that they have diverged sufficiently from the parent stem, accorded full and independent family status. If the latter step is adopted then, according to the argument of Davis and Griffiths, quoted above, a distinct family should be erected for each evolutionary line involved. Elevating all three lines to family rank would create two monogeneric families (the African and the East Indian) separable from the Bufonidae only by their so-called " arcifero-firmisternal " shoulder girdles.

* Parker (1934) was aware that *Hyperolius horstocki* has an incomplete ear condition for some time after metamorphosis (du Toit & de Villiers, 1932); he interpreted this, however, as an indicator that the condition is a phylogenetically primitive one.

TABLE 4

Species	Value of squamosal angle			
	Late larva	End of metamorphosis	Juvenile	Adult
Discoglossus pictus	60° (2)	55°	48°	40°
Megophrys hasselti	60 (12)	55		40
M. major	80 (10)	60	55	42
Cacosternum boettgeri	60 (3)	55	50	50
Ooeidozyga lima	70 (4)	60		50
Rana alticola	75 (3)	65	55	50
R. temporaria	75 (3)	70	58	50
R. tigrina	70 (5)	65		50
R. rugulosa	75 (6)	60		50
Staurois latutensis	65 (2)	58		50
Rhacophorus leucomystax	70 (3)	65	55	50
Calluela guttulata	65 (2)	62		50
Microhyla butleri	62 (2)	60	52	50
M. rubra	65 (4)	60	55	50
Hyla dominicensis	80 (6)	58		50
Bufo bufo	80 (3)	70	62	60
Dendrophryniscus stelzneri	76 (2)	68		65

The number in brackets under the larval stage indicates the length of the tadpole tail in millimetres.

But, as has already been emphasized, criteria based on the degree of fusion of the epicoracoids are incapable of exact taxonomic application. I therefore propose that the range of the Bufonidae be extended to include forms with varying degrees of epicoracoid fusion provided it is not complete, and that the Atelopodidae be redefined to accommodate only those genera where the cartilages are fused along their mesial edges up to the posterior limits of the coracoids. The latter family thus consists of *Atelopus* and *Brachycephalus* only, whilst *Cacophryne*, *Dendrophryniscus*, *Didynamipus* and *Oreophrynella* are retained as generic levels within the parent stock. This step makes the positions of *Dendrophryniscus* and *Oreophrynella* more satisfactory than if they were allocated to the Atelopodidae for, although both genera are obviously allied to *Bufo*, their relationships to one another are not at all clear.

B. Rhinodermatinae

Within this group are currently placed *Geobatrachus*, *Rhinoderma* and *Sminthillus*. The position of the latter has already been discussed. It has also been noted that, hitherto, the shoulder girdle of *Rhinoderma* has been incorrectly described: its epicoracoids are free from one another posteriorly and extend backwards as epicoracoid horns on each side of the sternum (Fig. 14). The possession by the genus of dorsal and ventral pulvinaria vocale, a ventral insertion for the hyoglossus muscle and a prezonal element to the pectoral girdle excludes the Bufonidae as the ancestral stock. The origin of the genus should probably be sought in the Leptodactylidae although, at present, no evidence is available to indicate where in this family the immediate stem stock should be sought.

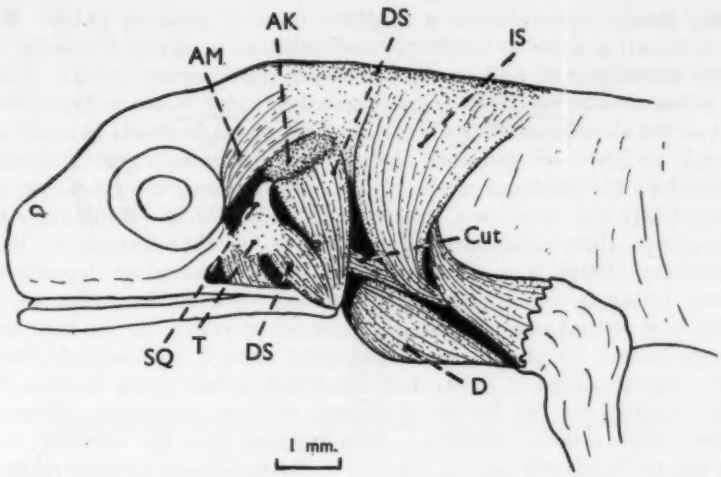

Fig. 17.—*Rana temporaria*. Lateral view of the depressor mandibular muscle in a froglet eight months after metamorphosis. (Key to lettering, p. 486.)

Geobatrachus is a rare monospecific genus inhabiting the higher altitudes of the Santa Marta Mountains in Colombia. Scarcity of material made a histological examination impossible but the genus is certainly not a dendrobatid as Ruthven (1915) claimed : maxillary teeth are present and the epicoracoids are free to the same degree as those of *Rhinoderma*. One of its characteristics are the curious pointed digital dilations and reduced inner finger and toe. These points recall the condition in *Euparkerella brasiliensis* (=*Sminthillus brasiliensis* Parker, 1926) and this may possibly indicate the origin of the genus.

These rhinodermatid genera differ from the leptodactylid frogs only as the atelopodid forms (except *Atelopus* and *Brachycephalus*) differ from the Bufonidae : they possess a deeper precoracoid bridge so that the degree of freedom and overlap displayed by the mesial edges of the epicoracoid cartilages is variously reduced but never completely lost. It is proposed, therefore, that the Leptodactylidae be redefined to accommodate the species hitherto designated as the Rhinodermatinae.

C. Dendrobatinae

This subfamily includes three genera only : *Dendrobates*, *Hyloxalus* and *Phyllobates*. Noble (1922, 1926, 1931) derived them from the leptodactylid *Crossodactylus* because of their procoelous vertebrae, their thigh complex, their digital scutes and because he believed that "*Phyllobates subpunctatus* normally passes through an arciferal, and arcifero-firmisternal and a firmisternal condition in the course of its ontogeny". But it has already been shown that the vertebral pattern has not the exact taxonomic validity vested in it by Noble, and, in any event, the synsacral condition in *Dendrobates* allies it no more with the procoelous than the diplasiocoelous forms. The argument that

synsacry should be considered a modified form of procoely (which Noble's views demand) is quite untenable as the condition occurs in *Philautus romeri* (present investigation) and in *Rana curtipes* (Ramaswami, 1933). Furthermore, it has already been shown that *Hyloxalus*, which Noble and most authors regard as the stem genus, has a thigh complex which is ranoid in every detail. Although, as has been indicated above, major taxonomic groups should not be defined on the evidence of the thigh complex alone, the character, nevertheless, clearly has value as a pointer to the direction of evolutionary trends within groups whose relationship is well defined by other characters. Parker's investigation (1940) thus shows clearly, in the Australian leptodactylids, that the primitive condition of the semitendinosus tendon, relative to the gracilis, is a ventral one with a trend towards dorsality in the later-evolved more specialized forms. If, as is generally agreed, *Hyloxalus* is the stem genus of the dendrobatid frogs, then the trend in this group inclines from a ranoid towards (but so far as is known without completely achieving) a bufonoid thigh muscle condition. This suggests that the ancestry of these forms should be sought among the ranoid, firmisternous families rather than among the leptodactylids as Noble proposed. This view is supported by the fact that the tendon of the semitendinosus in both *Phyllobates* and *Dendrobates* (Fig. 16) still lies dorsal to the massive factor of the gracilis major and differs from *Hyloxalus* and ranoids only in being overlain by the very tenuous gracilis minor.

Ranoid affinities are also indicated by the occurrence in all these forms of a *bursa angularis oris* (Fuchs, 1931 ; de Villiers, 1931) and by the development and nature of the pectoral girdle. The *bursa angularis oris* is a lymphocytic accumulation lying in the angle of the mouth between the maxillary and pterygoid bones. Its occurrence has constantly been reported in firmisternal genera (de Villiers, 1931 ; Ramaswami, 1939) but never, so far as the author is aware, in arciferal species. Noble's claim that *Phyllobates* has an arciferal stage cannot be upheld : examination of larval stages of *Phyllobates subpunctatus* and *P. trinitatus* shows that at no time do the epicoracoid cartilages overlap, but the adult condition is established well before the end of metamorphosis as in typical firmisternal forms. Furthermore, the adult shoulder girdle of the Dendrobatinae differs from that in species belonging to or derived from the Arcifera in not possessing epicoracoid horns and their associated musculature ; these persist even when the derived line achieves complete firmisterny and, as in the case of *Brachycephalus* (Fig. 18), even when the sternum is lost.

Another argument employed by Noble for deriving the dendrobatid line from the Leptodactylidae is the occurrence in all three genera of so-called " leathery scutes " on the upper surface of each digit tip. These are really glandulo-muscular organs and probably function to facilitate adhesion to foliage etc. Comparable pads are found, also, in *Crossodactylus* and Noble interpreted this as an indicator of relationship. It should be recalled, however, that identical pads occur in the petropedetid ranids (Pl. 4, fig. 13).

Ranoid affinities are further suggested by the group's very distinctive breeding behaviour : all three genera lay their eggs on land but have aquatic

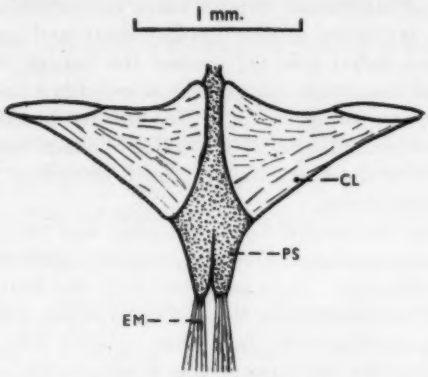

Fig. 18.—*Brachycephalus epihippium*. Ventral view of the epicoracoid horns and their muscles. (Key to lettering, p. 486.)

larvae which are transported to the pools on the backs of the paternal parents (Ruthven, 1915 ; Dunn, 1957). Such breeding habits are found in no other Salientia except in the arthroleptid ranids (Brauer, 1898),* a group which, significantly, is particularly labile with regard to its vertebral pattern (Nicholls, 1916 ; Noble, 1922 ; and present investigation), lacks vomerine teeth and, in some species, exhibits a cartilaginous instead of a bony sternum. These are all characters which, from purely theoretical considerations, would be expected in the dendrobatid stem stock and two interpretations seem possible. Firstly, the South American species may have evolved in the African tropics and subsequently dispersed. Secondly, the geographic pattern may reflect a true diphylety and the two groups may have evolved from two distinct, generalized ranid stocks residing in the same general regions as their present-day descendants. Which of these is the correct interpretation is a matter for future research involving, particularly, life-history data, breeding behaviour, calling etc. What is clear is that the South American genera can no longer be allied with the bufonoids. I propose, therefore, that the Dendrobatinae be redefined as a neotropical subfamily of the Ranidae. They are distinguished by (*a*) the presence of a firmisternal shoulder girdle, a prezonal element and, on the dorsal surface of each digit, a pair of "dermal scutes" and (*b*) by the absence of vomerine teeth, intercalary phalanges, a bony sternum and epicoracoid horns with their associated musculature.

SUMMARY

1. The morphology of the thigh complex, pectoral girdle, depressor musculature of the jaw, hyolaryngeal apparatus and urogenital system is described in *Sminthillus limbatus*. The latter system in the female is unique among all known Salientia in that the left Mullerian duct is vestigial.

* A recent examination of the Seychelles "pelobatids" indicates that they are specialized ranids. This report will be published independently.

2. The validity of taxonomic criteria based on vertebral pattern, myology, osteology and the structure of the hyolaryngeal and urogenital system is evaluated. It is concluded that (*a*) neither the nature of the vertebrae nor the arrangement of the thigh complex is a reliable character on which to define major salientian categories and (*b*) criteria based on the degree of freedom of epicoracoid cartilages are incapable of exact taxonomic application. The Arcifera and Firmisternia are redefined according to the presence or absence of epicoracoid horns.

3. The phylogeny of *Sminthillus* is analysed and the three species (*brasiliensis*, *limbatus* and *peruvianus*) are considered to represent three independent eleutherodactylid offshoots. It is proposed that the Peruvian and Brazilian forms, respectively, be generically designated *Noblella* and *Euparkerella* with the retention of *Sminthillus* for the Cuban species only. The re-allocation of the three genera to the Leptodactylidae is advocated.

4. The relationships of the brachycephalid frogs are reviewed. It is proposed that

(*a*) the Atelopodidae be defined to accommodate only firmisternal forms (*Atelopus* and *Brachycephalus*) and that range of the Bufonidae (*sensu stricto*) be extended to accommodate the remaining genera hitherto included in the Atelopodinae,

(*b*) genera currently included in the Rhinodermatinae be transferred to the Leptodactylidae and the latter family redefined to include so-called " arcifero-firmisternal " forms,

(*c*) the dendrobatid genera *Dendrobates*, *Hyloxalus* and *Phyllobates* be redefined as a neotropical subfamily of the Ranidae.

These propositions are supported by the evidence of comparative morphology and breeding behaviour.

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EXPLANATION OF THE PLATES

PLATE 1

Fig. 1.—*Sminthillus limbatus*. Transverse section at level "A" text-fig. 2.
„ 2.—*Sminthillus limbatus*. Transverse section at level "A" text-fig. 3.
„ 3.—*Sminthillus limbatus*. Transverse section at level "B" text-fig. 2.
„ 4.—*Sminthillus limbatus*. Transverse section at level "D" text-fig. 3.

PLATE 2

Fig. 5.—*Sminthillus limbatus*. Frontal section through the hyolaryngeal apparatus at the level of the tracheal processes.
„ 6.—*Sminthillus limbatus*. Frontal section through the hyolaryngeal apparatus at the level of the dorsal pulvinaria.
„ 7.—*Sminthillus limbatus*. Frontal section through the hyolaryngeal apparatus between the levels of the tracheal and bonchial processes.
„ 8.—*Rana rugulosa*. X-ray photograph of the pectoral girdle. Ventral view of froglet immediately after the completion of metamorphosis.

PLATE 3

Fig. 9.—*Sminthillus limbatus*. Transverse section at level "A" of text-fig. 10.
„ 10.—*Sminthillus limbatus*. Transverse section showing the transition from the convoluted to the smooth epithelium in the ovisac.
„ 11.—*Rhinoderma darwini*. Transverse section at level "A" of text-fig. 14.

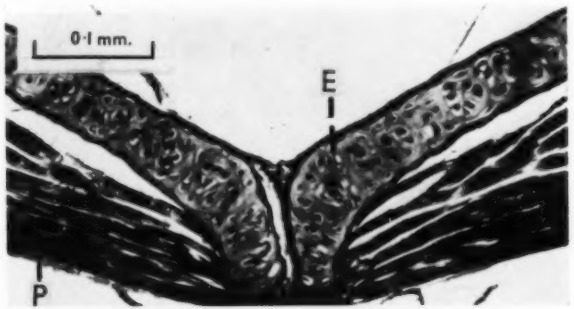
PLATE 4

Fig. 12.—Transverse section at level "C" of text-fig. 10.
„ 13.—*Petropedetes johnstoni*. Transverse section through a digital pad.
„ 14.—*Rana temporaria*. Lateral view of alizarin stained preparation showing the value of the squamosal angle at metamorphosis.
„ 15.—*Philautus romeri*. Ventral view of vertebral column showing synsacry.

KEY TO THE LETTERING OF THE FIGURES

A	arytenoid.
AC	articulating process of the cricoid.
AK	auditory capsule.
AM	musculus adductor magnus.
B	boundary between the convoluted and smooth areas of the ovisac lining.
BL	bladder.
BP	bronchial process of cricoid.
C	musculus cruralis.
CC	convoluted epithelium of the left half of the ovisac.
CD	coracoid.
CK	cloaca.
CO	common ovisac.
CL	crico-arytenoid ligament.
CLA	musculus constrictor laryngis anterior.
CLE	musculus constrictor laryngis externus.
CP	cardiac process of cricoid.
CR	cricoid.
CU	point at which the common Wolffian duct is cut and the posterior portion reflected back.
CV	clavicle.
D	musculus deltoideus.
DB	dorsal sternal blade.
DF	factor of the depressor mandibulae arising from the dorsal fascia.
DG	dorso-medial groove.

DIL musculus dilator laryngis.
DS factor of the depressor mandibulae arising from the squamoso-otic arch.
E epicoracoid cartilage.
EHR right epicoracoid horn.
EM muscle of the epicoracoid horn.
F convoluted region of the ovisac lining.
FH epicoracoid horn lying free from the sternum.
G mucous cells.
GM musculus gracilis major.
GN musculus gracilis minor.
H hyale.
HCL hyo-cricoid ligament.
HGL musculus hyoglossus.
HP hyoid plate.
I sternal isthmus.
IH musculus interhyoideus.
IM musculus intermandibularis.
IS musculus infraspinatus.
K knee capsule.
L left coracoid bone.
LO left oviduct.
LR lumen of right oviduct.
LU left Wolffian duct.
M middle mucous layer.
MC muscle capsules.
MX maxilla.
NS unconvoluted region of ovisac.
O lumen of ovisac.
OA outer adventitia.
OE musculus obliquus externus.
OH m. omohyoideus.
OL lumen of ovisac.
OP oesophageal process of the cricoid.
P pectoralis muscle.
PA musculus petrohyoideus anterior.
PL postero-lateral process of the hyoid.
PMP postero-medial process of the hyoid.
PP musculus petrohyoideus posterior.
PV pulvinaria vocale.
PZ prezonal element.
Q quadrato-jugal.
R right epicoracoid cartilage.
RA musculus rectus abdominis.
RO right oviduct.
RU right Wolffian duct.
S musculus semitendinosus.
SG sternal groove.
SH musculus sternohyoideus.
SQ squamosal.
SS sternal stem.
T tympanic area.
TG tendon of the gracilis.
TH thyroid gland.
TP tracheal process of the cricoid.
TR transition point from convoluted to smooth epithelium.
TS tendon of the semitendinosus.
U union of the rectus abdominis with the epicoracoid horn muscle.
UE unfolded epithelium in the right half of the ovisac.
V vestige.
VB ventral sternal blade.
VC vocal chord.
W unconvoluted region of ovisac lining.
X septomaxilla.
Y ilium.
Z urostyle.



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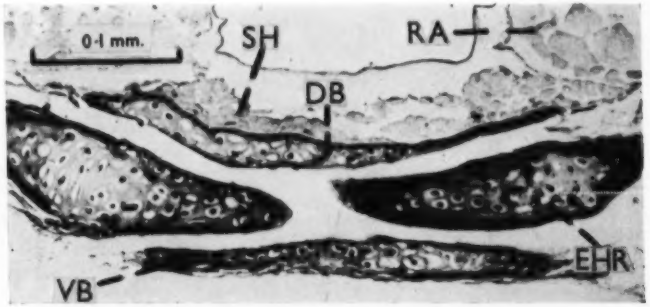

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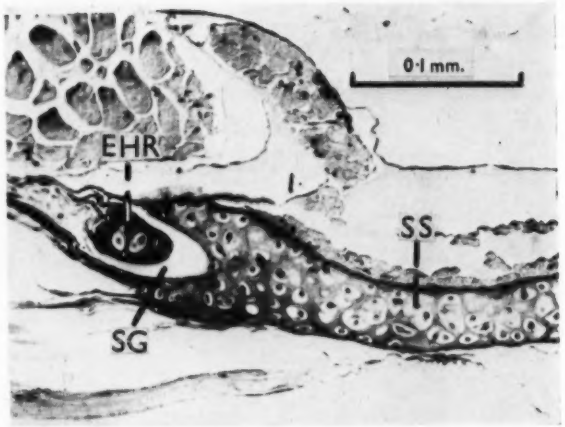

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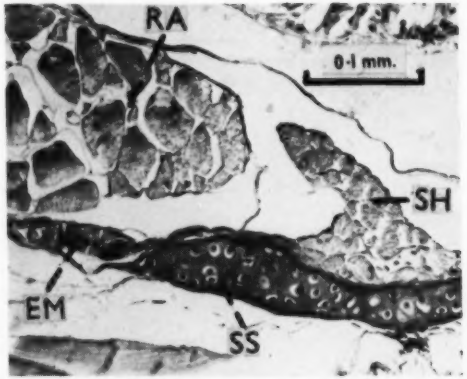

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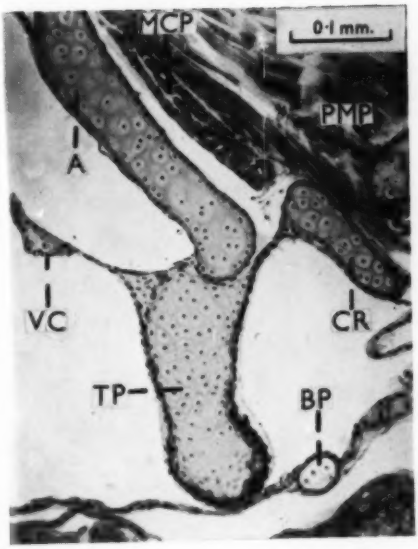
The phylogeny of *Sminthillus limbatus*.



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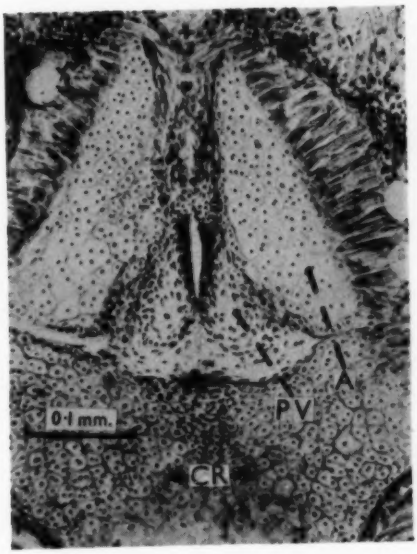

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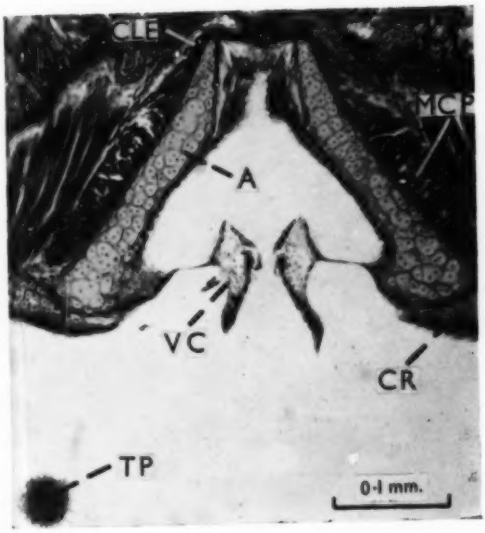

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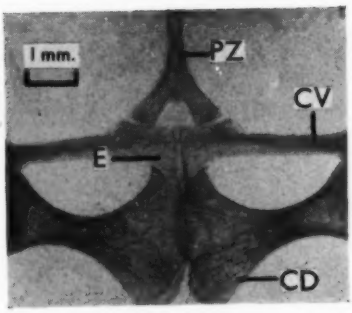

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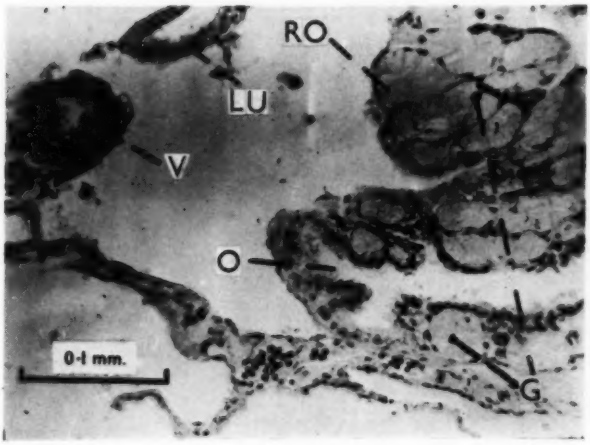

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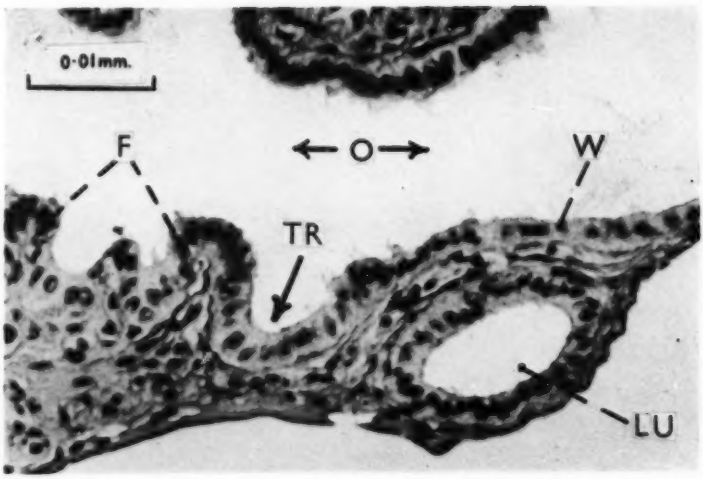

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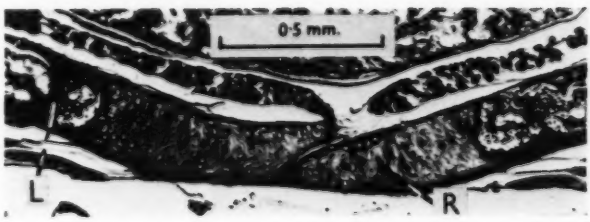

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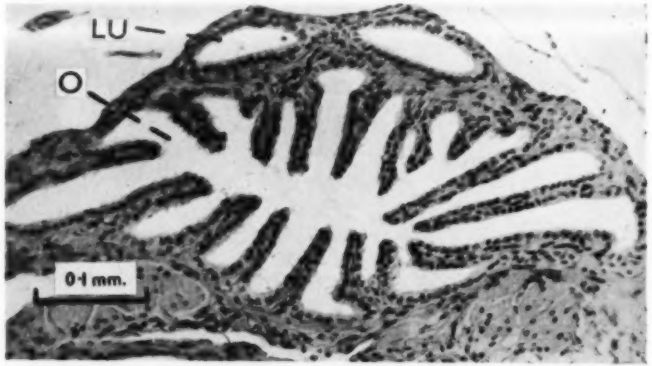

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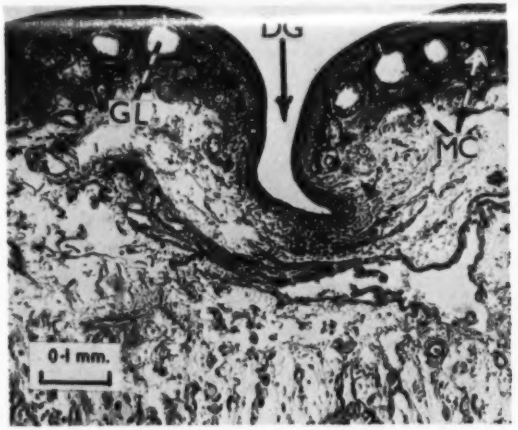

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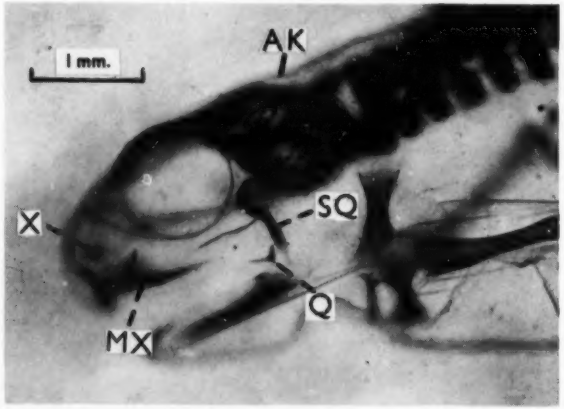

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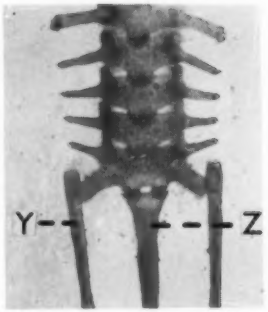

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The phylogeny of *Sminthillus limbatus*.

THE NUMBERS OF EXHIBITS, BIRTHS AND DEATHS IN THE MENAGERIE AT REGENT'S PARK: 1835–1957, AND IN WHIPSNADE PARK: 1931–1957

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(With 3 figures in the text)

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FOREWORD

When trying to discover what substance there was to a number of statements about mortality and birth rates in the Society's collections, to which wide publicity was given in the National Press, I made a preliminary analysis of the vital statistics of Regent's Park and Whipsnade. The results of this analysis, which were incorporated in the Report of the Council of the Society for 1957, showed that, contrary to view that mortality rates are now rising and birth rates falling in the Regent's Park Gardens, the reverse is the case.

Since this was only a preliminary analysis, I suggested to Dr Ashton and Dr Vevers that they might undertake a more detailed study of the Society's vital statistics. The results are incorporated in the present paper.

The three main indices studied are:

(*a*) Numbers of vertebrates exhibited;

(*b*) Birth rates; and

(*c*) Mortality rates.

Numbers of animals obviously fluctuate from year to year, according to the amount of space we have available; according to the financial resources we can use when competing with numerous new, as well as old, Zoological Gardens; and according to the availability of the animals themselves. Many creatures which were represented in the Society's collections a hundred, and even fifty, years ago are now well-nigh extinct in the wild. Our numbers also vary with changing policy with regard to group exhibitions. For example, for reasons of policy we no longer keep in Regent's Park either a large colony of Hamadryad baboons (*P. hamadryas*) or of rhesus monkeys (*M. mulatta*).

The frequency of births is again to a large extent accidental. As pointed out in the paper, the Society's statistics of birth rates are not true measures of the reproductive potentialities of our animals. In some cases only a single representative of any one species may have been represented at a time; in others, we may not have had two mature specimens of opposite sexes at the same time; in others again, lack of space would have prevented the housing of males and females together.

The index which stands out most clearly as a mark of the Society's progress in the field of animal husbandry, which we can justly claim is subject to stricter and stricter scientific control as every year passes, is clearly that of mortality, which gives a measure of the health of our animals. This index fell steadily from the beginning of the century until the early 1930's, and then showed a tendency to rise through the Second World War, and the post-war years. To-day it is declining steeply, a change which reflects not only the value of the new hospital and pathological services which we brought into operation three years ago, but also the increasing use of modern clinical methods in the care of our animals. We do not know, and it is possible we shall never know, the natural longevity of most of the animals in our collection. We can only go on hoping, therefore, that this index will continue to fall.

S. ZUCKERMAN

INTRODUCTION

In addition to the customary statements of the numbers of vertebrates exhibited during the year, and of the numbers of births and deaths in the Gardens at Regent's Park and at Whipsnade Park, the Society's report for 1957 provided a summary account of recent trends in the size of the collections and in the birth and mortality rates. Attention was first drawn to the fact that the total numbers of exhibits have tended to rise since the end of the Second World War, a planned decline in the numbers at Regent's Park being more than offset by an increase of stock at Whipsnade. So far as concerns the numbers of species and subspecies exhibited, the collections, it was noted, remain " more representative than most, and probably than any other Zoo in the world ".

In 1956, the birth rate among mammals, birds, reptiles and amphibians taken together was approximtely 10 per 100 exhibits in the Regent's Park menagerie—this figure having remained practically constant since 1953 and being some 4 units higher than in 1946. The 1956 figure was also some 3 units higher than the level usual in the 1920's, a period when the menagerie was undergoing considerable development. In the case of mortality, it was pointed out that whereas the index among mammals, birds, reptiles and amphibians averaged 30·5 between 1948 and 1953, by the time the 1957 report was compiled, it had fallen to 27·5.

The purpose of the present study is to examine, so far as the available data allow, the changes which have occurred since the Society's incorporation in 1829, and especially during the past twelve years, first in the size and composition of the collections, and second in the birth and death rates in the major vertebrate groups.

MATERIALS AND METHODS

Sources of data

Number of exhibits

Except for the years 1842–1846 and 1850–1858 the Society's reports have, since 1835, contained an annual statement of the number of vertebrates (excluding fish) exhibited in the Gardens at Regent's Park. Corresponding figures for Whipsnade Park are available since its opening in 1931.

With the exception of the years already noted, separate totals were published year by year until 1922 for the numbers of (*a*) mammals; (*b*) birds, and (*c*) reptiles and amphibians. Subsequently, only the overall figure is given, but the annual valuation lists of the stock have enabled the overall total for each of the past twelve years (1946–1957) to be subdivided. In the case of birds and mammals, a further separation has been made into wild species as distinct from those which are commonly domesticated in Great Britain. These latter comprise among the birds: budgerigars and canaries together with domestic varieties of pigeons, fowl, ducks and geese; and among the mammals: guinea pigs, ferrets, ponies, donkeys and rabbits, together with domestic varieties of sheep, oxen, pigs and goats.

The numbers of wild mammals exhibited in each of the past twelve years have been finally split into subtotals for the sixteen orders represented in the collections.

Number of species and subspecies

The numbers of wild species and subspecies in the collections can be assessed from the annual valuation sheets, and for the purpose of the present study, counts were made for each of the last seven years.

Number of births

From 1867 onwards, detailed lists were published in each annual report of the numbers and species of mammals, birds, reptiles and amphibians bred in the Gardens. For the twelve years between 1946 and 1957, births among wild species of mammals and birds have been separated from those in species commonly domesticated in Great Britain. Births among wild mammals have also been classified order by order.

Number of surviving births

Between 1867 and 1910 the annual lists recorded all animals that were born, irrespective of the length of time that each survived. From 1911 onwards and with the exception of 1946 and 1947 each annual report shows whether or not the animal was reared to the end of the calendar year.

The unpublished data for 1946 and 1947 were compiled from the detailed index of recent breeding records kept in the Society's Offices. Animals born in the menagerie, and sold before the end of the calendar year, have been regarded as survivors.

Number of deaths

The number of deaths in the menagerie is given by the number of carcases brought to the Prosectorium or Pathology Department, for post mortem

examination. With few exceptions, in the years before 1928, the reports give only the total number of vertebrate deaths, but subsequently subtotals have been published for mammals, birds, reptiles and amphibians.

For each of the twelve post-war years (1946–1957), the numbers of deaths in wild and domesticated species of mammals and birds have been assessed by reference to the detailed post mortem records. For this period, counts have also been made of the numbers of post mortem examinations carried out year by year on wild representatives of each mammalian order.

Nature of data

The data used in this study are subject to the following qualifications:

Number of exhibits

The available data relate to the numbers of exhibits on December 31st of each year, and these, owing to fluctuations in the size of the collections, do not necessarily represent the average strength for the year. To that extent they correspond to the Ministry of Agriculture's June returns.

Mention has already been made of certain gaps in the records of vertebrate numbers during the early years of the Society's history. Between 1923 and 1945, subtotals for mammals, birds, reptiles and amphibians are not available. Finally, records sufficiently detailed to permit a breakdown into taxonomic groups smaller than classes or to permit a separation between wild and domesticated species are available only for the period following the Second World War. Consequently, even although more detailed information could be obtained for the numbers of births and deaths, correspondingly detailed values of derived indices could not be computed for the period: 1923–1945.

Number of births

Several accidental factors operate to prevent the breeding of captive animals (Zuckerman, 1953), and the numbers of births recorded year by year are not, therefore, true measures of the reproductive potentialities of colonies of the size represented by the crude totals published in the annual reports. Thus, in some cases, only a single representative of any one species may have been exhibited, while in others, lack of space will have prevented the housing of males and females together. Again, the annual lists of exhibits do not differentiate between adult and immature specimens, and many of those included will not have reached reproductive age.

In earlier years it was customary to record all births, but more recently only those which survived for a few days have been listed.

Lists of births are not available for the years before 1867, and whereas before 1922 the tables comprised practically entirely wild species, subsequently domesticated species of mammals and birds have been included. The prolific breeding of a number of these—notably guinea pigs and budgerigars—has tended to inflate the total numbers of births. For the years 1946–1957, however, it has been possible to separate wild and domestic species for the purpose of analysis.

Number of surviving births

Those animals which are born in the menagerie during any one year, and which survive until December 31st, will, by that date, have lived for a variable length of time and will not necessarily have reached maturity. The percentage which has only lived for a limited period, or alternatively which has not by the end of the year reached maturity will, however, within the limits of sampling error, be the same in each year. The figures recorded in the annual reports therefore provide a good indication of variations that occur from year to year in the proportion of surviving births.

Number of deaths

Although at Regent's Park all dead animals are brought to the Pathology Laboratory, in the free-ranging colonies in Whipsnade Park, the numbers of deaths among wild fowl which fly into the enclosures in which bears and wolves are kept cannot be estimated.

Annual publication of the total number of post mortem examinations began only in 1883. There are gaps for the years 1901, 1905–1907 and 1915–1924, while, with isolated exceptions, subtotals for mammals, birds and reptiles are only given subsequent to 1927.

Analysis

Extent of analysis

Analyses were made of all available figures relating to the numbers of exhibits, births and deaths except those for the years 1914–1918 and 1939–1945, when, as a result of the two World Wars, the numbers of exhibits in the Society's collections were deliberately reduced. Few new animals were obtained, and those remaining comprised mainly the longer-lived and more valuable types. Figures for the birth and death rates during these periods are not, therefore, comparable with those for the remaining years.

For the years after the opening of Whipsnade Park, separate analyses were made (*a*) for the animals at Regent's Park and (*b*) for those in the two collections combined.

Composition of collections

After preliminary studies of variations in the total numbers of vertebrates exhibited year by year, together with those in the numbers of mammals, birds, reptiles and amphibians, examinations were made of annual variations in the proportion of the total collection accounted for by each of these groups. For the period 1946–1957, additional analyses were made, first of the proportions of wild and domestic varieties of birds and mammals in the total vertebrate collections, and second in the percentage of the collection of wild mammals accounted for by representatives of each order.

Indices of numbers of births, survivals and deaths

In order to relate the numbers of births and deaths to the corresponding numbers of exhibits, the following indices were, whenever possible, computed

(*a*) for all vertebrates (less fish), (*b*) for reptiles and amphibians, (*c*) for wild and domestic birds, (*d*) for wild birds alone, (*e*) for wild and domestic mammals, (*f*) for wild mammals alone and (*g*) for the various orders of wild mammals:

(i) $\dfrac{100 \times \text{number of births}}{\text{Number of exhibits}}$ (i.e. the birth rate)

(ii) $\dfrac{100 \times \text{number of births that survived to the end of the year}}{\text{Total number of births}}$ (i.e. the survival rate)

(iii) $\dfrac{100 \times \text{number of deaths}}{\text{Number of exhibits}}$ (i.e. the mortality rate)

Statistical analysis

Trends of change in the number of exhibits, in the composition of the collections and in each of the three indices, were defined by fitting linear regressions to the data, the significance of their slopes being assessed in the usual way.

Mean values of corresponding indices for different vertebrate groups or for Regent's Park and Whipsnade were compared by means of t tests and analyses of variance.

RESULTS

Tables

The results of the analysis are summarised in Tables 1–11. Table 1 records fluctuations that have occurred during the past 122 years in the numbers of vertebrates exhibited in the Gardens. Between 1835 and 1938, average values are, so far as the available data allow, presented for each period of five years but as variations during the twelve years following the Second World War are of special significance relative to the present-day development of the Gardens, averages are given for each of the three-yearly periods: 1946–1948, 1949–1951, 1952–1954, together with individual figures for 1955, 1956 and 1957. Table 2 gives corresponding information for the numbers of wild representatives of the various mammalian orders exhibited between 1946 and 1957. Table 3 lists the numbers of wild species and subspecies exhibited year by year between 1951 and 1957. The remaining pairs of tables are arranged in a form similar to that adopted in tables 1 and 2. Thus, tables 4 and 5 relate to changes in the proportion of the collections accounted for by mammals, birds or reptiles and amphibians, 6 and 7 to changes in the birth rate, 8 and 9 to variations in the survival rate and 10 and 11 to those in the mortality rate.

Number of exhibits

Present-day state (Table 1)

The numbers of exhibits have, during the past nine years remained practically stable, averaging approximately 5000. This level is similar to

TABLE 1

Numbers of vertebrate exhibits: 1835–1957.

Year	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
Regent's Park and Whipsnade								
1931–1935	—	—	—	—	4706	—	—	—
1936–1938	—	—	—	—	5232	—	—	—
1946–1948	3905	1009	1974	922	4264	1215	2127	922
1949–1951	4542	1106	2627	809	4863	1284	2770	809
1952–1954	4423	1177	2525	721	4912	1463	2728	721
1955	4488	1199	2601	688	5150	1544	2918	688
1956	4318	1255	2479	584	4944	1498	2862	584
1957	4301	1354	2444	503	4889	1563	2823	503
Regent's Park								
1835–1841	—	—	—	—	961	300	639	22
1847–1849	—	—	—	—	1108	361	707	40
1859–1865	—	—	—	—	1659	474	1056	129
1866–1870	—	—	—	—	2025	570	1285	170
1871–1875	—	—	—	—	2119	626	1270	223
1876–1880	—	—	—	—	2194	639	1370	185
1881–1885	—	—	—	—	2420	723	1388	309
1886–1890	—	—	—	—	2383	678	1345	360
1891–1895	—	—	—	—	2420	685	1379	356
1896–1900	—	—	—	—	2667	818	1365	484
1901–1905	—	—	—	—	2688	707	1480	501
1906–1910	—	—	—	—	3082	846	1733	503
1911–1913	—	—	—	—	3644	833	2259	552
1919–1920	—	—	—	—	2530	575	1475	480
1921–1925	—	—	—	—	3251	—	—	—
1926–1930	—	—	—	—	3860	—	—	—
1931–1935	—	—	—	—	3832	—	—	—
1936–1938	—	—	—	—	3764	—	—	—
1946–1948	2819	644	1417	758	3058	795	1505	758
1949–1951	3313	717	1852	744	3518	860	1914	744
1952–1954	3015	684	1678	653	3277	873	1751	653
1955	2887	612	1654	621	3298	856	1821	621
1956	2798	620	1662	516	3147	780	1851	516
1957	2584	618	1539	427	2900	769	1704	427

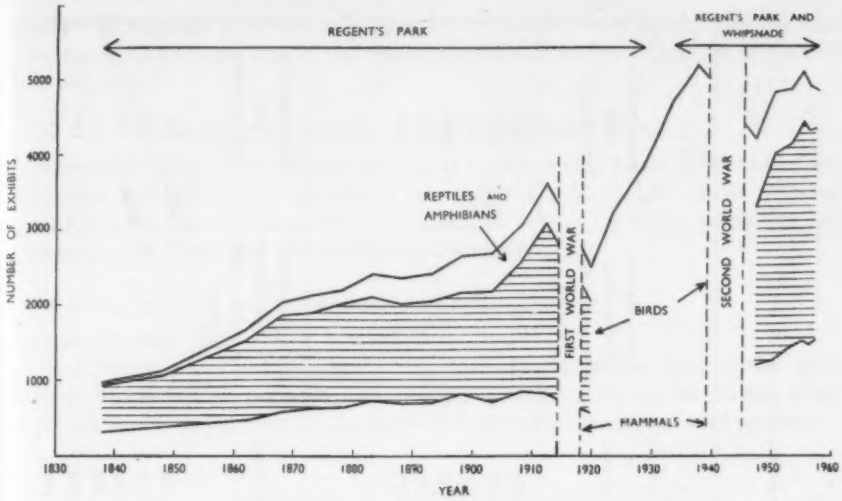

Fig. 1.—Variation in numbers of exhibits: 1835–1957.

that attained during the years immediately before the Second World War, and is higher than at any other time during the 120 years for which records are available.

The mammalian exhibits now number 1560 of which 1350 are from wild species. These figures represent the maxima yet recorded for this group.

Growth of menagerie (Tables 1 and 2)

Before 1840, fewer than 1000 vertebrates were, on an average, exhibited each year. The numbers increased progressively, there being an average of 2000 by 1870, 2700 by the turn of the century and 3600 in the years preceding the outbreak of the First World War.

During the First World War, the total number of exhibits fell to some 2500, but in the years before 1931—the year when Whipsnade Park was opened—the stock at Regent's Park had been increased to an average of 3900 animals. Subsequently, although the numbers in the London menagerie tended to deline—e.g. as a result of reduction in the size of such groups as the primate colony on 'Monkey Hill'—the development of Whipsnade Park resulted in the total collections containing, by the outbreak of the Second World War, more than 5000 exhibits.

During the Second World War, the total numbers of vertebrates fell, there being at the end of 1945 only 2700 exhibits in the combined collections. Of these 1850 were in Regent's Park. After the war, the collections at both Regent's Park and Whipsnade were rapidly built up, the average vertebrate strength for the period 1946–1948 being 4300 for the combined collections. This figure increased to 4900 during the following three years.

After 1951, the numbers at Regent's Park were, as a matter of policy, gradually reduced and stand today at approximately the 1946 level. The

TABLE 2

Numbers of exhibits in various mammalian orders (wild species only): 1946–1957.

Regent's Park and Whipsnade							
Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	98	15	171	154	222	12	337
1949–1951	86	21	183	172	232	11	401
1952–1954	106	19	208	138	233	9	464
1955	134	14	138	147	226	12	528
1956	122	14	133	175	239	11	561
1957	129	11	146	193	217	10	648
Regent's Park							
Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	17	15	155	140	169	8	140
1949–1951	23	21	168	162	179	8	156
1952–1954	22	19	185	126	169	4	159
1955	20	14	110	127	163	7	171
1956	21	14	106	142	174	6	157
1957	30	11	114	155	146	5	157

numbers of exhibits in Whipsnade Park have, on the other hand, been allowed to increase, so that the size of the combined collections has remained at around 5000 exhibits.

Number of species and subspecies exhibited (Table 3)

There has been little change during the past seven years in the numbers of species and subspecies exhibited, the total for mammals, birds, reptiles and amphibians fluctuating around a mean of 1200. Of these, some 300 are mammals, 700 birds and 200 reptiles and amphibians.

Composition of collections

Present-day state (Tables 1, 2, 4 and 5)

At present, mammals account for approximately 30 per cent of the total exhibits, birds for 60 per cent and reptiles and amphibians for 10 per cent. Approximately 90 per cent of the birds and mammals are from wild species.

TABLE 3

Numbers of wild species and subspecies in the collections: 1951–1957.

Regent's Park and Whipsnade							
Year	1951	1952	1953	1954	1955	1956	1957
Mammals	279	282	283	282	270	285	277
Birds	694	703	732	771	773	727	734
Reptiles and amphibians	221	227	212	240	233	196	168
Total	1194	1212	1227	1293	1276	1208	1179
Regent's Park							
Year	1951	1952	1953	1954	1955	1956	1957
Mammals	256	258	260	255	247	259	247
Birds	667	675	701	738	739	687	691
Reptiles and amphibians	219	225	210	238	230	193	166
Total	1142	1158	1171	1231	1216	1139	1104

Past changes in composition (Tables 1, 2, 4 and 5)

During the past century, the most striking changes in the composition of the collections, have concerned the proportion of the total exhibits accounted for by reptiles and amphibians. Initially, this group comprised only 2 per cent of the collection, but the figure increased progressively until by the turn of the century it had become approximately 20 per cent—a value which remained reasonably stable until 1914. The proportion of birds but not of mammals was, in the years before 1900, reduced correspondingly. After the turn of the century, the proportion of mammals declined, while that of birds increased. By the outbreak of the First World War, this latter group accounted for some 60 per cent of the total exhibits.

TABLE 4

Percentage distribution of vertebrate exhibits: 1835–1957.

Year	Wild species only			Wild and domestic species		
	Mammals	Birds	Reptiles and amphibians	Mammals	Birds	Reptiles and amphibians
Regents' Park and Whipsnade						
1946–1948	25·8	50·6	23·6	28·5	49·9	21·6
1949–1951	24·4	57·8	17·8	26·4	57·0	16·6
1952–1954	26·6	57·1	16·3	29·8	55·5	14·7
1955	26·7	58·0	15·3	30·0	56·7	13·3
1956	29·1	57·4	13·5	30·3	57·9	11·8
1957	31·5	56·8	11·7	32·0	57·7	10·3
Regent's Park						
1835–1841	—	—	—	31·2	66·5	2·3
1847–1849	—	—	—	32·6	63·8	3·6
1859–1865	—	—	—	28·6	63·6	7·8
1866–1870	—	—	—	28·1	63·5	8·4
1871–1875	—	—	—	29·6	59·9	10·5
1876–1880	—	—	—	29·1	62·5	8·4
1881–1885	—	—	—	29·9	57·3	12·8
1886–1890	—	—	—	28·5	56·4	15·1
1891–1895	—	—	—	28·3	57·0	14·7
1896–1900	—	—	—	30·7	51·2	18·1
1901–1905	—	—	—	26·3	55·1	18·6
1906–1910	—	—	—	27·5	56·2	16·3
1911–1913	—	—	—	22·9	62·0	15·1
1919–1920	—	—	—	22·7	58·3	19·0
1946–1948	22·8	50·3	26·9	26·0	49·2	24·8
1949–1951	21·6	55·9	22·5	24·5	54·4	21·1
1952–1954	22·7	55·6	21·7	26·7	53·4	19·9
1955	21·2	57·3	21·5	26·0	55·2	18·8
1956	22·2	59·4	18·4	24·8	58·8	16·4
1957	23·9	59·6	16·5	26·5	58·8	14·7

TABLE 5

Percentage distribution of mammalian exhibits (wild species only): 1946–1957.

Regent's Park and Whipsnade							
Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	9·7	1·5	16·9	15·3	22·0	1·2	33·4
1949–1951	7·8	1·9	16·5	15·6	21·0	1·0	36·2
1952–1954	9·0	1·6	17·7	11·7	19·8	0·8	39·4
1955	11·2	1·2	11·5	12·3	18·8	1·0	44·0
1956	9·7	1·1	10·6	13·9	19·1	0·9	44·7
1957	9·5	0·8	10·8	14·3	16·0	0·7	47·9
Regent's Park							
Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	2·6	2·3	24·1	21·7	26·3	1·3	21·7
1949–1951	3·2	2·9	23·4	22·6	25·0	1·1	21·8
1952–1954	3·2	2·8	27·1	18·4	24·7	0·6	23·2
1955	3·3	2·3	18·0	20·8	26·6	1·1	27·9
1956	3·4	2·2	17·1	22·9	28·1	1·0	25·3
1957	4·9	1·8	18·4	25·1	23·6	0·8	25·4

Apart from figures for 1919–1920, data for the inter-war years are not available. Following the Second World War, the proportion of mammals in the collections had, due to their forming a relatively large proportion of the exhibits in Whipsnade Park, again risen to approximately 25 per cent—a figure which has continued to rise slightly during the past twelve years. The proportion of birds in the two collections had, by 1946, fallen to about 50 per cent of the total exhibits, this figure subsequently increasing to about 60 per cent at the present day.

These increases in the proportion of mammals and birds have been counterbalanced by a fall in that of reptiles and amphibians, the figure for this group falling from 20 per cent immediately after the Second World War to 10 per cent at the present day.

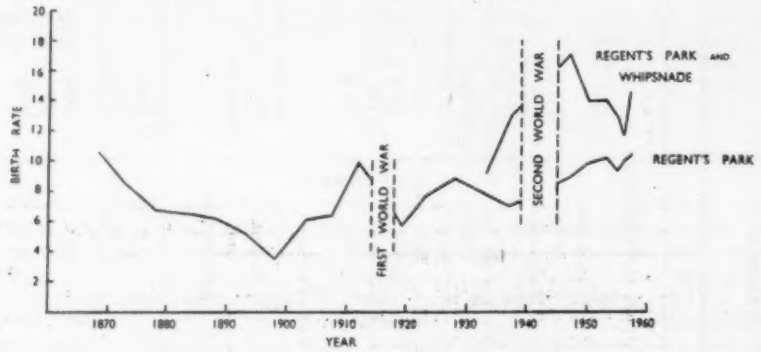

Fig. 2.—Variation in birth rate: 1867–1957. The rise in birth rate between 1939 and 1945 may be attributed to the fact that during the Second World War the collections contained an increasingly large proportion of animals that had become fully acclimatized to life in captivity.

Birth rate

Present-day state (Tables 6 and 7).

The birth rate, in wild and domesticated species in the combined collections at Regent's Park and Whipsnade, now stands at more than 14. This figure is greater than for any part of the period for which records are available except for the years between 1946 and 1948 when the birth rate was inflated to 17 as a result of the collections containing an exceptionally high proportion of animals which had lived in the menagerie throughout the Second World War and which had become completely acclimatized to life in captivity. In Regent's Park alone, the birth rate was, during 1957, 10·4. This value too, is one of the highest ever recorded in this section of the collection.

When only wild species are considered, the 1957 figures for the entire collections and for the exhibits in Regent's Park fall to 11·8 and 5·8 respectively. These too are close to the maximum figures recorded for wild species during the post-war period.

TABLE 6

Birth rates: 1867–1957.

Year	Regent's Park and Whipsnade							
	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1931–1935	—	—	—	—	9·2	—	—	—
1936–1938	—	—	—	—	12·9	—	—	—
1946–1948	13·6	18·8	15·0	5·3	17·0	23·8	18·1	5·3
1949–1951	11·5	17·3	12·5	0·9	13·9	22·0	14·1	0·9
1952–1954	10·7	17·6	10·0	1·7	14·0	26·7	10·4	1·7
1955	9·7	20·2	7·0	1·5	12·8	28·0	7·4	1·5
1956	9·4	19·4	6·1	1·4	11·6	23·6	7·3	1·4
1957	11·8	22·1	8·5	0·0	14·4	24·7	11·3	0·0

Year	Regent's Park							
	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1867–1870	—	—	—	—	10·6	9·6	12·3	1·3
1871–1875	—	—	—	—	8·5	7·2	10·0	3·0
1876–1880	—	—	—	—	6·7	6·0	6·6	10·6
1881–1885	—	—	—	—	6·5	8·9	4·4	9·8
1886–1890	—	—	—	—	6·2	10·5	4·7	3·6
1891–1895	—	—	—	—	5·2	8·7	3·6	5·4
1896–1900	—	—	—	—	3·5	6·0	3·1	0·9
1901–1905	—	—	—	—	6·1	7·1	7·2	1·0
1906–1910	—	—	—	—	6·4	7·0	6·9	3·8
1911–1913	—	—	—	—	9·9	10·6	10·0	9·0
1919–1920	—	—	—	—	5·7	6·3	5·2	6·3
1921–1925	—	—	—	—	7·6	—	—	—
1926–1930	—	—	—	—	8·8	—	—	—
1931–1935	—	—	—	—	7·7	—	—	—
1936–1938	—	—	—	—	7·0	—	—	—
1946–1948	4·7	10·6	1·4	6·3	8·9	17·3	5·8	6·3
1949–1951	5·9	9·9	6·3	1·0	9·8	18·3	9·4	1·0
1952–1954	6·0	9·9	5·9	1·9	10·2	25·0	5·9	1·9
1955	4·4	9·2	3·6	1·6	9·3	27·7	3·3	1·6
1956	5·7	9·5	5·5	1·6	10·0	20·3	8·0	1·6
1957	5·8	7·4	6·7	0·0	10·4	16·1	10·4	0·0

Past changes in index (Tables 6 and 7)

During the late 1860's the numbers of births per 100 vertebrates exhibited stood at approximately 10. This figure declined steeply during the subsequent thirty-five years until, at the turn of the century, it was only 4 per 100 exhibits. This decline was due mainly to the progressively smaller numbers of birds born in the menagerie, the index for this group falling during the period from 12 to 3. There were no correspondingly marked changes in the indices for mammals or reptiles.

Before the outbreak of the First World War, the birth rate in all groups tended to rise, and by 1913 the overall index had almost regained its earlier average value of 10.

By the end of the 1914 War, the birth rate in all groups had dropped markedly, the figure for 1919–1920 being less than 6. By the time Whipsnade Park was opened in 1931, this had again risen to almost 9. So far as can be judged from the available data, this increase was due in large measure to the prolific breeding of a number of domesticated species, especially budgerigars, which had not figured previously in the lists of births.

During the years following the opening of Whipsnade Park (1931–1938), the birth rate in the collections as a whole increased to a value of 13. This change was due mainly to high breeding rates at Whipsnade, those in the London Gardens tending, if anything, to decline.

Between 1946 and 1948 the overall birth rate for Regent's Park and Whipsnade averaged 17—a figure which, for reasons already noted, was higher than in 1938. The corresponding value for the period 1949–1951 was 14. The birth rate has subsequently oscillated around this level which is somewhat higher than in pre-war years.

Several marked changes have also occurred during the post-war period first in the birth rates for mammals, birds and reptiles, and second in the Society's two collections. Thus, at Regent's Park, a slight decline in the birth rate for reptiles and amphibians and among wild mammals (especially rodents) has been offset by an increase in the figures for wild birds and in those for domestic mammals. This has resulted in a slight upward trend in the overall birth rates in the Gardens. At Whipsnade, practically the reverse changes have occurred. The birth rate among wild mammals (especially ungulates) has increased, but that among the wild birds has fallen and given a slight overall downward trend for the combined collections. This decline in the numbers of hatchings per 100 birds exhibited at Whipsnade has resulted mainly from the continued introduction throughout the past ten years of species (e.g. egret, flamingo, ibis) which seldom breed in captivity, and which, because of their unusual interest, have formed an ever increasing proportion of the exhibits. Coupled with this, there has been a deliberate restriction of breeding in certain groups (e.g. pheasants) which have, throughout, been well represented in the collection.

Group variation in birth rate

Regent's Park and Whipsnade: Since 1931, the birth rates in the free-ranging colonies in Whipsnade Park have been consistently higher than in

the more closely-confined groups in the menagerie at Regent's Park, the difference for the post-war years averaging 16 units.

Mammals, birds and reptiles: Throughout the period for which records are available, the birth rate among reptiles and amphibians has been highly variable and is, on an average, less than 50 per cent of that for birds and mammals. Differences also occur between the birth rates for these two groups. In the earliest phases of the Society's history, the index for birds tended to exceed that for mammals. During the twentieth century, however, the figures for mammals have averaged approximately twice those for birds.

TABLE 7

Birth rates in various mammalian orders (wild species only): 1946–1957.

Year	Regent's Park and Whipsnade				
	Monotremata and Marsupialia	Primates	Rodentia and Lagomorpha	Carnivora	Perissodactyla and Artiodactyla
1946–1948	60·8	2·2	16·3	21·5	16·0
1949–1951	68·1	2·4	17·6	12·7	16·9
1952–1954	53·3	2·8	15·5	11·9	20·0
1955	41·8	5·8	4·8	29·6	19·3
1956	35·2	4·5	13·1	18·4	22·8
1957	42·6	6·8	7·3	25·3	25·5

Year	Regent's Park			
	Primates	Rodentia and Lagomorpha	Carnivora	Perissodactyla and Artiodactyla
1946–1948	2·0	17·8	14·7	10·0
1949–1951	2·4	18·1	7·8	13·0
1952–1954	3·2	16·9	8·7	14·2
1955	6·4	5·5	13·5	9·9
1956	1·9	14·8	7·5	11·5
1957	0·0	6·5	13·0	10·8

Mammalian orders: Apart from marsupials, where, as a result of the high birth rate among the wallabies in Whipsnade Park, the indices are exceptionally big (average 56), the highest birth rates occur in ungulates (19), carnivores (18) and rodents (14). The corresponding figures for primates and insectivores are 3 and 6 respectively.

Survival rate (Tables 8 and 9)

Present-day state

During 1957, more than 90 per cent of the animals born survived to the end of the calendar year. The figures for the entire collections and those for wild species alone are similar, and are close to the corresponding values

for the two preceding years, the average for the three being bigger than during any corresponding period since the opening of Whipsnade Park in 1931.

The figures for wild and domestic species in Regent's Park are, with the exception of the years between 1926 and 1930, on an average higher, during the past three years, than at any time since records first became available in 1911. The values for wild species are now as high as the maximum previously attained.

Past changes in index

The index for the years immediately following the First World War (85) was some 6 units greater than between 1911 and 1913. Between 1919 and

TABLE 8

Survival rates: 1911–1957.

Regent's Park and Whipsnade								
Year	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1931–1935	78·4	80·4	91·0	41·8	83·8	82·2	95·2	41·8
1936–1938	78·5	81·8	88·6	30·2	81·5	84·0	91·1	30·2
1946–1948	77·1	80·4	79·3	63·8	80·3	81·4	82·8	63·8
1949–1951	90·4	85·6	94·1	76·3	91·5	88·4	94·5	76·3
1952–1954	88·3	83·5	91·9	90·4	90·4	88·7	92·4	90·4
1955	90·6	86·0	96·7	90·0	92·4	90·3	96·7	90·0
1956	91·6	91·4	94·7	37·5	93·4	93·8	94·8	37·5
1957	90·5	88·3	93·7	—	92·3	90·7	94·3	—
Regent's Park								
Year	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1911–1913	78·5	68·5	86·7	63·8	79·2	69·0	87·3	63·8
1919–1920	85·1	68·8	85·9	97·1	85·4	68·8	86·9	97·1
1921–1925	82·1	81·3	91·7	23·8	85·6	81·3	93·6	23·8
1926–1930	90·4	86·5	95·5	100·0	95·7	86·5	99·3	100·0
1931–1935	75·1	79·5	93·9	41·8	81·4	79·5	97·2	41·8
1936–1938	58·8	64·7	79·4	30·2	65·9	66·8	90·6	30·2
1946–1948	66·7	70·9	81·5	63·8	77·5	75·5	91·6	63·8
1949–1951	82·2	71·1	89·7	76·3	87·7	83·9	92·4	76·3
1952–1954	82·3	71·0	88·1	90·4	88·1	87·8	88·0	90·4
1955	81·7	67·9	93·3	90·0	89·6	89·0	91·8	90·0
1956	84·8	79·7	93·4	37·5	91·4	91·8	94·0	37·5
1957	91·3	95·7	89·3	—	93·4	96·8	91·0	—

the opening of Whipsnade Park, the indices for mammals and birds rose progressively, the overall value for vertebrates in the years before 1931 averaging 90 units. A corresponding change occurred in the wild species of birds and mammals.

The overall survival rate tended to decline between the opening of Whipsnade Park and the outbreak of the Second World War. This resulted from a decrease first, in the numbers of surviving births among birds at both Regent's Park and Whipsnade, and second, in those of mammals in the Gardens at Regent's Park. These outweighed an increase in the survival rate of the mammals at Whipsnade. However, in the case of wild species alone, the overall survival rate for the two parks combined remained, during this period, practically stable at around 78.

Although during the years immediately following the war, the overall figure for the combined collections remained at the pre-war level of about 80, that for Regent's Park increased from a pre-war value of 66 to one of 78 for wild and domestic species combined, and from 59 to 67 for wild species alone.

Throughout the past twelve years, the survival rates have risen not only in the Regent's Park menagerie, but also in the collections as a whole. This change has affected both wild and domestic species.

TABLE 9

Survival rates in various mammalian orders (wild species only): 1946–1957.

Regent's Park and Whipsnade					
Year	Monotremata and Marsupialia	Primates	Rodentia and Lagomorpha	Carnivora	Perissodactyla and Artiodactyla
1946–1948	95·8	61·1	82·0	63·2	78·9
1949–1951	97·8	61·1	62·8	85·9	86·8
1952–1954	94·0	72·2	78·2	73·0	82·6
1955	96·4	62·5	71·4	79·1	89·2
1956	93·0	66·7	78·3	95·5	93·0
1957	96·4	70·0	92·9	98·2	83·6

Regent's Park			
Year	Rodentia and Lagomorpha	Carnivora	Perissodactyla and Artiodactyla
1946–1948	82·0	51·2	80·9
1949–1951	62·4	74·8	85·5
1952–1954	77·6	54·2	78·2
1955	71·4	63·6	76·5
1956	76·2	92·3	77·8
1957	100·0	94·7	94·1

Group variation in survival rate

Regent's Park and Whipsnade: The overall index of survival is, for the post-war years, on an average some 5 units bigger for the collections at Whipsnade than for those in the menagerie at Regent's Park. The difference is evident in both birds and mammals and is conspicuous in the cases of wild species.

Mammals, birds and reptiles: The survival rate for reptiles and amphibians is highly variable, but for the collections as a whole averages some 25 units less than in mammals, whose index is, in turn some 5 units lower than in

TABLE 10

Mortality rates: 1883–1957.

Regent's Park and Whipsnade								
Year	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1946–1948	26·8	30·9	20·5	38·0	26·5	29·5	20·5	38·0
1949–1951	25·6	26·1	19·4	45·0	25·3	25·0	19·7	45·0
1952–1954	24·5	26·7	18·5	41·6	23·8	25·3	18·2	41·6
1955	24·3	25·9	16·4	51·3	27·6	25·4	23·1	51·3
1956	25·5	20·6	19·6	61·1	24·3	19·3	19·4	61·1
1957	21·7	17·2	16·9	57·7	21·2	16·9	17·1	57·7
Regent's Park								
Year	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
1883–1885	—	—	—	—	42·3	—	—	—
1886–1890	—	—	—	—	38·6	—	—	—
1891–1895	—	—	—	—	39·0	—	—	—
1896–1900	—	—	—	—	44·2	—	—	—
1902–1904	—	—	—	—	51·9	—	—	—
1908–1913	—	—	—	—	48·1	—	—	—
1925–1930	—	—	—	—	31·5	—	—	—
1931–1935	—	—	—	—	25·1	—	—	—
1936–1938	—	—	—	—	27·2	—	—	—
1946–1948	32·6	38·2	24·0	45·4	32·5	36·2	24·6	45·4
1949–1951	30·5	31·2	22·8	48·9	30·5	29·5	23·8	48·9
1952–1954	30·3	36·8	21·8	45·9	30·0	35·1	22·2	45·9
1955	33·4	35·6	23·8	56·7	35·3	30·0	30·5	56·7
1956	31·2	26·9	21·4	68·0	30·0	24·0	21·9	68·0
1957	29·0	23·8	20·7	66·5	27·5	21·1	20·7	66·5

birds. In both mammals and birds, the index for wild and domestic species combined is, on an average, similar to that for wild varieties alone.

Mammalian orders: For the past twelve years, the survival rate for the entire collection of marsupials has averaged 96, for perissodactyls and artiodactyls 84, for rodents 76, for carnivores 75 and for primates 65.

Mortality rate (Tables 10 and 11)

Present-day state

During 1957, the mortality rate for the collections of vertebrates at Regent's Park and Whipsnade stood at 21. This value is the lowest yet recorded. The corresponding figure for vertebrates in Regent's Park alone is 28, this representing a lower death rate than at any time since the Second World War.

The mortality rate in wild species is very similar to that in wild and domestic species combined, and the present-day values for wild species, both in the entire collection and in the Regent's Park Gardens alone, are less than at any time since the Second World War.

Past changes in index

From an initial value in 1883 of approximately 40, the index increased to more than 50 by the turn of the century. This figure had not declined noticeably by the outbreak of the First World War. Records for the years

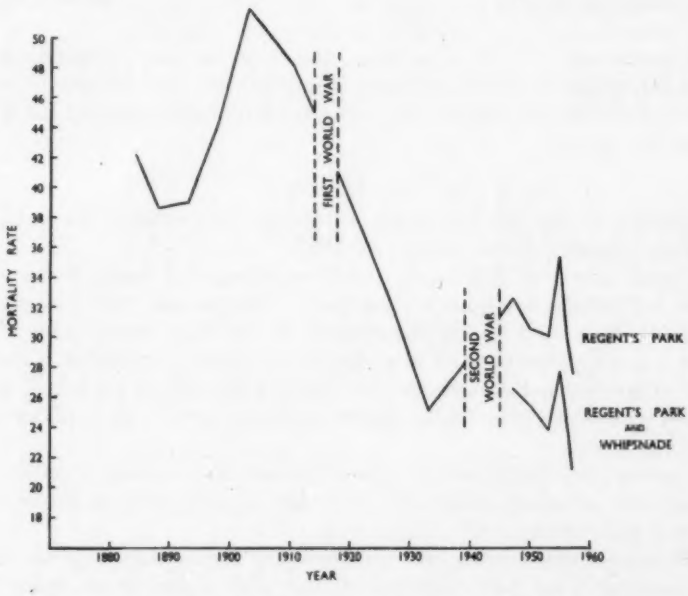

Fig. 3.—Variation in mortality rate: 1883–1957.

1919–1924 have not been preserved, but for the period 1925–1930 the index had fallen to 32. Its value then declined, the average figure for the period 1936–1938 being 27.

In the years immediately following the Second World War, the figure for the entire collection was still at approximately the same level, although the index for the Gardens in Regent's Park had risen to 33. Subsequently, the tendency, in both the entire collection and in Regent's Park, has been for the index to decline, levels for recent years being, as already noted, among the lowest in the Society's history. This post-war decrease in mortality has been most conspicuous in the case of wild mammals, the index for the collections as a whole falling from an average value of 31 for the years 1946–1948, to one of 17 in 1957. A decrease from 21 to 17 units has occurred in birds, but in the case of reptiles and amphibians the tendency has been for the index of mortality to increase, this being largely due to the temporary inclusion in the collection of a number of short-lived amphibians.

Group variation in mortality rate

Regent's Park and Whipsnade: Throughout the post-war period, the mortality rate in Whipsnade Park has averaged some 20 units less than in the Gardens at Regent's Park. The difference between the two Parks is not only evident in both birds and mammals as a whole, but also occurs in many mammalian orders.

Mammals, birds and reptiles: During the past twelve years, the index has, in reptiles, and amphibians, been highly variable, averaging approximately 50. That for mammals has, in the entire collection, averaged 25, while the corresponding value for birds is lower still, amounting to only 20.

Mammalian orders: On an average, the index is least in ungulates (15), of intermediate size in carnivores and primates (25), and biggest in rodents and insectivores (50–65), these types being relatively short-lived in nature (e.g. tree frogs and newts).

CONCLUSION

The results of the present analysis confirm and extend the indications given in the Society's annual report for 1957.

The total stock of mammals, birds, reptiles and amphibians in the combined collections at Regent's Park and in Whipsnade Park has, with the exception of the period during the Second World War, stood, since the mid 1930's at a level higher than at any time in the Society's history. The total numbers of species and subspecies have, during the period for which records have been analysed (1951–1957), shown nothing more than random annual fluctuations.

The present-day birth rate in the collections as a whole is close to the maximum ever attained, while the birth rate among wild mammals is now higher than ever before.

In the case of wild species, the percentage of births surviving to the end of the calendar year has, throughout the past three years, been bigger than ever before, while in the collections as a whole, the survival rate has,

TABLE 11

Mortality rates in various mammalian orders (wild species only): 1946–1957.

Regent's Park and Whipsnade

Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	36·0	80·9	29·8	52·0	34·4	32·3	17·7
1949–1951	20·2	62·9	35·3	50·6	23·9	15·2	13·3
1952–1954	22·1	64·1	51·2	49·0	18·0	14·1	14·8
1955	20·1	78·6	47·1	44·2	29·2	8·3	14·2
1956	20·5	21·4	27·1	43·4	15·5	9·1	14·4
1957	13·2	54·5	21·9	27·5	23·5	10·0	11·3

Regent's Park

Year	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
1946–1948	53·9	80·9	31·3	57·3	41·8	41·7	19·5
1949–1951	37·7	62·9	29·2	52·6	28·1	24·5	12·3
1952–1954	58·9	64·1	57·1	51·2	21·8	30·0	18·4
1955	65·0	78·6	55·5	45·7	30·7	14·3	14·0
1956	38·1	21·4	29·2	52·1	16·1	16·7	14·0
1957	13·3	54·5	25·4	33·5	30·8	20·0	6·4

TABLE 12

Numbers of exhibits, together with birth rates, survival rates and mortality rates in vertebrate collections—1958·

	Regent's Park and Whipsnade							
	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians
Number of exhibits	4329	1312	2404	613	4871	1503	2755	613
Numbers of species and subspecies exhibited	1163	284	708	171	—	—	—	—
Percentage distribution of exhibits	100·0	30·3	55·5	14·2	100·0	30·9	56·5	12·6
Birth rate	10·3	17·4	9·0	0·0	14·5	22·8	13·1	0·0
Survival rate	89·2	83·8	94·9	—	92·3	88·3	96·1	—
Mortality rate	21·0	22·6	16·1	37·0	20·5	21·4	16·4	37·0
	Regent's Park							
	Wild species only				Wild and domestic species			
	All vertebrates less fish	Mammals	Birds	Reptiles and amphibians	All vertebrates less fish	Mammal	Birds	Reptiles and amphibians
Number of exhibits	2579	601	1447	531	2914	735	1648	531
Numbers of species and subspecies exhibited	1093	257	667	169	—	—	—	—
Percentage distribution of exhibits	100·0	23·3	56·1	20·6	100·0	25·2	56·6	18·2
Birth rate	6·0	9·2	7·0	0·0	12·9	22·4	12·8	0·0
Survival rate	86·5	78·2	91·1	—	92·8	90·9	94·3	—
Mortality rate	26·3	29·5	19·4	41·6	24·8	26·1	18·8	41·6

TABLE 13

Numbers of exhibits, together with birth rates, survival rates and mortality rates in various mammalian orders (wild species only)—1958.

	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
Regent's Park and Whipsnade							
Number of exhibits	123	24	145	181	217	7	615
Percentage distribution of exhibits	9·4	1·8	11·1	13·8	16·5	0·5	46·9
Birth rate	41·5	—	4·8	13·8	9·2	—	20·3
Survival rate	100·0	—	57·1	72·0	85·0	—	80·8
Mortality rate	21·1	16·7	27·6	32·0	22·6	0·0	19·5
Regent's Park							
	Monotremata and Marsupialia	Insectivora, Chiroptera, Edentata and Pholidota	Primates	Rodentia and Lagomorpha	Carnivora	Tubulidentata, Proboscidea, Hyracoidea and Sirenia	Perissodactyla and Artiodactyla
Number of exhibits	17	24	106	141	150	4	159
Percentage distribution of exhibits	2·8	4·0	17·6	23·4	25·0	0·7	26·5
Birth rate	—	—	1·9	12·1	3·3	—	18·9
Survival rate	—	—	50·0	64·7	40·0	—	93·3
Mortality rate	100·0	16·7	34·0	33·3	28·7	0·0	18·9

for the past nine years, remained at a level which had previously been exceeded only between 1926 and 1930.

The mortality rates in the combined vertebrate collections are now lower than ever before, the figures for 1956 and 1957 amounting to less than half the peak values recorded during the early years of the present century.

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SUMMARY

(1) Comparisons have been made, between the present-day conditions and those existing during earlier phases of the Society's history in respect to:

(*a*) the numbers of vertebrates (excluding fish) exhibited in the menagerie.

(*b*) the proportion of the total vertebrate exhibits accounted for by (i) mammals (ii) birds (iii) reptiles and amphibians.

(*c*) the birth rate.

(*d*) the survival rate of vertebrates born in the menagerie.

(*e*) the mortality rate.

(2) Apart from the period during the Second World War when the numbers of vertebrates dropped sharply, the collections have, since the mid-1930's, fluctuated around a level of some 5000 exhibits. The numbers of species and subspecies have, during the past seven years, varied slightly around an average of approximately 1200.

(3) Mammals now account for some 30 per cent of the total exhibits, birds for 60 per cent while reptiles and amphibians comprise 10 per cent. Approximately 90 per cent of the mammals and birds exhibited are from wild species.

(4) The birth rate in the collections as a whole now stands at 14 per 100 exhibits. The corresponding value for wild species is 11·8. These figures are among the highest attained during the periods for which records are available.

(5) More than 90 per cent of the animals born in the menagerie during 1957 survived to the end of the year. The average survival rate for the past three years is higher than at any time since the opening of Whipsnade Park in 1931.

(6) The mortality rate for the entire vertebrate collections stood, during 1957, at 21. This figure is less than at any time either before or after the Second World War.

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ADDENDUM (March, 1959)

The numbers of vertebrates alive in the Society's collections on 31st December 1958, together with figures for births and deaths during the preceding twelve months became known when this report was in the press. These data, together with derived indices, are summarized in Tables 12 and 13.

Both the numbers of vertebrates exhibited and the numbers of species and subspecies in the combined collections at Regent's Park and Whipsnade Park, have, during 1958, remained at the high levels recorded in recent years. As before, approximately 90 per cent of the vertebrate exhibits are from wild species, and there have been practically no changes in the proportions of the collections accounted for by the different vertebrate groups.

Birth rates in both the combined collections and in their subdivisions have, during the past twelve months, remained in the upper reaches of the high levels characteristic of the past four years, the indices for the wild species of birds and mammals exhibited in Regent's Park being the highest recorded for any phase of the post-war period.

The proportion of animals born in the Parks and surviving to the end of the calendar year has, as in previous years, stood at about 90 per cent.

The overall mortality rates in both the menagerie at Regent's Park and in the combined collections at Regent's Park and Whipsnade have continued to show a marked decline—a slight increase over the 1957 figures in the case of the mammals being more than offset by a fall in those for birds, reptiles and amphibians. The overall reduction in mortality is equally apparent when the figures for wild species are analysed apart from those for wild and domestic species combined.

NOTICE

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References thus appear as follows:—

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COWLES, R. B. (1956). Sidewinding locomotion in snakes. *Copeia* **1950**, 211.

ROMER, A. S. (1956). *Osteology of the reptiles.* Chicago.

GREEN, J. (1956). Variation in the haemoglobin content of *Daphnia*. *Proc. roy. Soc.* (B) **145**, 214.

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